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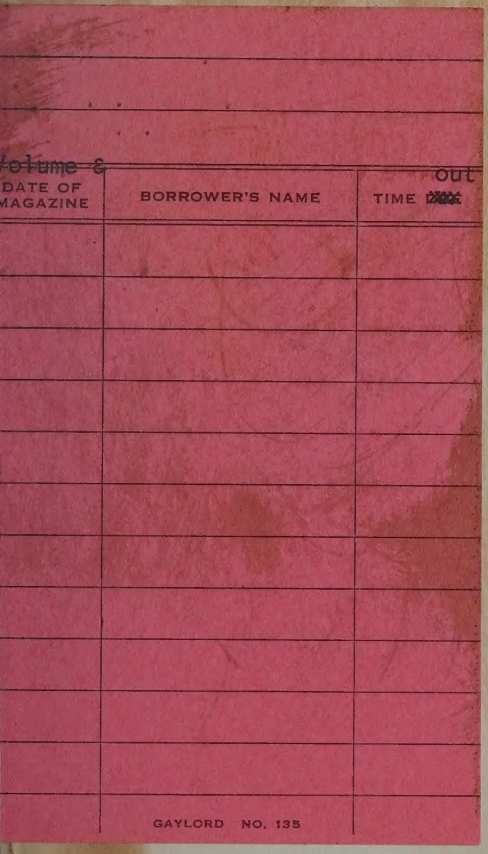
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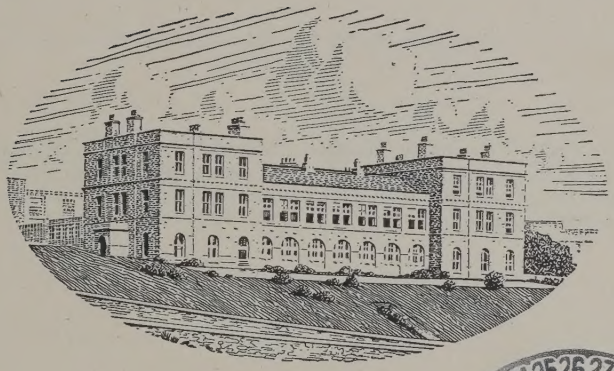

THE PLYMOUTH LABORATORY

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CONTENTS OF VOLUME XXIX

NUMBER 1, pp. 1–265, APRIL 1950
NUMBER 2, pp. 267–560, SEPTEMBER 1950
NUMBER 3, pp. 561–729, FEBRUARY 1951

PAGE

Report of the Council:
1949–50 519

Income and Expenditure Account and Balance Sheet:
1949–50 538

List of Governors, Founders, Members, Honorary and Associate Members: . . 541

Obituary:
Walter Garstang, 1868–1949 561

ARMSTRONG, F. A. J. and ATKINS, W. R. G.
The suspended matter of sea water 139

ARMSTRONG, F. A. J. and HARVEY, H. W.
The cycle of phosphorus in the waters of the English Channel. 145

ATKINS, W. R. G. and PARKE, MARY
Seasonal changes in the phytoplankton as indicated by chlorophyll estimations . 609

ATKINS, W. R. G.
See ARMSTRONG, F. A. J. and ATKINS, W R. G.

BAGENAL, T. B.
See BARNES, H. and BAGENAL, T. B.

BARNES, H.
A note on the barnacle larvae of the Clyde Sea Area as sampled by the Hardy Continuous Plankton Recorder 73

BARNES, H. and BAGENAL, T. B.
A statistical study of variability in catch obtained by short repeated hauls taken over an inshore ground 649

BARNES, H. and POWELL, H. T.
Some observations on the effect of fibrous glass surfaces upon the settlement of certain sedentary marine organisms 299

BLACK, W. A. P.
The seasonal variation in weight and chemical composition of the common British Laminariaceae 45
The seasonal variation in the cellulose content of the common Scottish Laminariaceae and Fucaceae 379

BURDON-JONES, C.
Observations on the spawning behaviour of *Saccoglossus horsti* Brambell & Goodhart, and of other Enteropneusta 625

PAGE

CARRUTHERS, J. N., LAWFORD, A. L. and VELEY, V. F. C.
Studies of water movements and winds at various lightvessels. II. At the Seven Stones Lightvessel near the Scilly Isles 587

CORBIN, P. G.
The occurrence of the smooth sand-eel, *Gymnammodytes semisquamatus* (Jourdain), in the Plymouth area, with notes on *G. cicerelus* (Rafinesque) and *G. capensis* (Barnard) 83

Records of pilchard spawning in the English Channel 91

DALES, R. PHILLIPS
The reproduction and larval development of *Nereis diversicolor* O. F. Müller . . 321
See WELLS, G. P. and DALES, R. PHILLIPS.

DIGBY, P. S. B.
The biology of the small planktonic copepods of Plymouth 393

FRETTER, VERA
Observations on the life history and functional morphology of *Cerithiopsis tubercularis* (Montagu) and *Triphora perversa* (L.) 567

GAULD, D. T.
The grazing rate of planktonic copepods 695
See RAYMONT, J. E. G. and GAULD, D. T.

HARVEY, H. W.
On the production of living matter in the sea off Plymouth 97
See ARMSTRONG, F. A. J. and HARVEY, H. W.

HILL, D. K.
Advances in the physiology of peripheral nerve 241

HOLME, N. A.
The bottom fauna of Great West Bay 163
Population-dispersion in *Tellina tenuis* da Costa 267
The identification of the British species of the genus *Ensis* Schumacher (Lamellibranchiata) 639

KNIGHT, MARGERY and PARKE, MARY
A biological study of *Fucus vesiculosus* L. and *F. serratus* L. 439

KNIGHT-JONES, E. W. and STEVENSON, J. P.
Gregariousness during settlement in the barnacle *Elminius modestus* Darwin . . 281

LAWFORD, A. L.
See CARRUTHERS, J. N., LAWFORD, A. L. and VELEY, V. F. C.

MENON, M. DEVIDAS
Bionomics of the poor-cod (*Gadus minutus* L.) in the Plymouth area. 185

MILLAR, R. H.
Lissoclinum argyllense n.sp., a new ascidian from Scotland 389

NICOL, J. A. C.
Response of *Branchiomma vesiculosum* (Montagu) to photic stimulation 303

PARKE, MARY
Notes on the Plymouth marine flora. Algal records for the Plymouth region . . 257
See ATKINS, W. R. G. and PARKE, MARY
See KNIGHT, MARGERY and PARKE, MARY

PAGE

POWELL, H. T.
See BARNES, H. and POWELL, H. T.

RAYMONT, J. E. G. and GAULD, D. T.
The respiration of some planktonic copepods 681

REES, W. J.
The distribution of *Octopus vulgaris* Lamarck in British waters. 361

SERGEANT, D. E.
The status of the common seal (*Phoca vitulina* L.) on the East Anglian coast . . 707

SPOONER, G. M.
Notes on the Plymouth marine fauna. Amphipoda. 247
Notes on the Plymouth marine flora. Additional records of *Laminaria ochroleuca* De la Pylaie 261

STEVEN, G. A.
Notes on the Plymouth marine fauna. Pisces 254

STEVENSON, J. P.
See KNIGHT-JONES, E. W. and STEVENSON, J. P.

VELEY, V. F. C.
See CARRUTHERS, J. N., LAWFORD, A. L. and VELEY, V. F. C.

VEVERS, H. G.
Ophiopsila annulosa (M. Sars) in the Plymouth area 81
The biology of *Asterias rubens* L. II. Parasitization of the gonads by the ciliate *Orchitophrya stellarum* Cépède 619

WELLS, G. P.
The anatomy of the body wall and appendages in *Arenicola marina* L., *A. claparedii* Levinsen and *A. ecaudata* Johnston 1

WELLS, G. P. and DALES, R. PHILLIPS
Spontaneous activity patterns in animal behaviour: the irrigation of the burrow in the polychaetes, *Chaetopterus variopedatus* Renier and *Nereis diversicolor* O. F. Müller 661

WOODWARD, F. N.
The Scottish Seaweed Research Association 719

Notes on the Plymouth marine fauna
See SPOONER, G. M.; STEVEN, G. A.

Notes on the Plymouth marine flora
See PARKE, MARY; SPOONER, G. M.

ABSTRACTS OF MEMOIRS RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

Ricerche su *Asterina gibbosa* (Penn.). I. La migrazione delle gonadi. II. L'ermafroditismo in uno popolazione di Plymouth. By Guido Bacci 263
Some new Myxosporidia from Plymouth with a proposed new classification of the order. By Yogendra R. Tripathi 264
The function of the giant axon of *Myxicola infundibulum* Montagu. By J. A. C. Nicol 265

PAGE

Conduction velocity in relation to axon diameter in *Myxicola infundibulum*. By J. A. C. Nicol, C. N. Smyth and D. Whitteridge 265

The annelid phosphagen: with a note on phosphagen in Echinodermata and Protochordata. By E. Baldwin and W. H. Yudkin 515

The effect of temperature on the electric activity of the giant axon of the squid. By A. L. Hodgkin and B. Katz 516

The effect of calcium on the axoplasm of giant nerve fibres. By A. L. Hodgkin and B. Katz 516

The effect of sodium ions on the electrical activity of the giant axon of the squid. By A. L. Hodgkin and B. Katz 516

Internode lengths in the nerves of fishes. By P. Kynaston Thomas and J. Z. Young . 517

The equilibrium function of the otolith organs of the Thornback Ray. By Otto Lowenstein and T. D. M. Roberts 727

The control of retinal pigment migration in *Leander serratus*. By Francis G. W. Knowles. 727

BOOK REVIEW

Nets. How to make, mend and preserve them. By G. A. Steven 729

ERRATA

VOL. XXIX

Page 166. Fig. 1. The legends for the two types of stipple indicating the *Turritella* ground should be transposed.

174. The sieve mesh for Station 26 is 1 mm. *not* 11 mm.

271. Fig. 2 is incorrectly placed and should be turned through 90° to the right so that the left-hand edge is at the top.

393. Insert *Acartia clausi* Giesbrecht in line 10 of the introduction.

626. Line 30. For *townshendii* read *townsendii*.

696. Line 30. For *Ditylium* read *Ditylum*.

703. Line 14. For *Ditylium* read *Ditylum*.

704. One line from bottom. For *Ditylium* read *Ditylum*.

705. Lines 3, 8. For *Ditylium* read *Ditylum*.

THE ANATOMY OF THE BODY WALL AND APPENDAGES IN *ARENICOLA MARINA* L., *ARENICOLA CLAPAREDII* LEVINSEN AND *ARENICOLA ECAUDATA* JOHNSTON

By G. P. Wells

Department of Zoology, University College, London

(Text-figs. 1–21)

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CONTENTS

	PAGE
Introduction	1
Methods	3
The main regions of the body	5
The body wall and appendages	9
The general structure of the body wall	9
The middle region ('trunk')	14
The anterior region ('head')	25
The posterior region ('tail')	37
Summary	41
References	42
Appendix: list of abbreviations used in the text-figures	44

Introduction

The anatomy of *Arenicola* has often been monographed. The best-known works are those of the series with which the names of Gamble and Ashworth are associated (Gamble & Ashworth, 1898, 1900; Ashworth, 1904, 1912). Unfortunately, these accounts are not fully satisfactory. They are sometimes incorrect; they omit all reference to many points of considerable functional interest; and they lack descriptive rigour (for example, although Gamble & Ashworth, 1900, point out that the blood vessels of *Arenicola* are arranged on an obvious segmental plan, none of these works attempts to bring out the fact by adopting a nomenclature based on serial homology). Now the lugworm is an excellent laboratory polychaete, and, because of its size, abundance and hardiness (at least during the cooler months), affords suitable material for many researches. A revision of its general anatomy is therefore desirable. The following account of the body wall and appendages was undertaken as a contribution to this end; a study of the internal anatomy is in preparation.

My first intention was to limit the description to *A. marina*, the commonest species around Great Britain and the one with which I am most familiar. On reflexion, however, the decision was taken to include two other species as well. The family Arenicolidae consists (according to Ashworth, 1912, with whose classification subsequent authorities are in substantial agreement) of two

genera only, *Arenicola* and *Branchiomaldane*. The first is made up of eight species, to which Berkeley & Berkeley (1939) have subsequently added a ninth; they fall quite clearly, from an anatomical point of view, into three groups. The second consists only of a single species of small and aberrant animals. Now to describe only *Arenicola marina* would result in a work of very limited usefulness, more particularly as the species is restricted to the cooler shores of the northern hemisphere; on the other hand, by including the three species *marina* L., *claparedii* Levinsen[1] and *ecaudata* Johnston, each representing one of the sections into which the genus naturally falls, an idea can be given of the general organization and also the range of variation found in this world-wide group. I hope later to publish notes on the other species; briefly, *grubii* most nearly resembles *ecaudata*, *assimilis* is most closely related to *claparedii*, though differing from it in several important points, and the rest group themselves with *marina*.

The descriptions are based mainly on material collected by myself—*marina* at Plymouth, at Bangor, North Wales, and at Thorpe Bay on the Thames Estuary; *claparedii* at Naples, where my expenses were partly defrayed by a grant from the Challenger Society; and *ecaudata* at Plymouth. I have also a small number of *claparedii* from the Pacific Coast of U.S.A., sent, very ill-preserved, by an American dealer. By the courtesy of Mr H. W. Parker I have been allowed to examine the collection of Arenicolidae in the British Museum (Natural History); this remains, with a few additions, substantially as catalogued by Ashworth (1912).

The following study is concerned with gross morphology, not histological detail. As far as possible, some indication will be given of the functional significance of the structures described. With *marina*, the habits of the worm are well known and such interpretations can often be made. This species lives in great numbers in muddy sand flats, where the piles of sandy cylinders, its faeces, and the saucer-shaped or funnel-shaped depressions, caused by its eating away the sand below, are familiar to everybody. It sometimes occurs in less typical habitats, for example, in gravel or among stones, provided there is a certain amount of muddy material to eat. Under favourable conditions, it inhabits the same burrow for weeks or even months at a stretch, swallowing the sand at one end of the burrow and depositing it as faeces at the other. The form of the burrow, and the behaviour of the worm, have been described in detail elsewhere (Wells, 1945, 1949*b*, 1950; Newell, 1948).

[1] *A. claparedii* Levinsen is probably identical with *A. pusilla* Quatrefages. The original definition of the latter species is inadequate and conflicts with the characters of the type specimen. The type was examined by Ashworth, who identified it as an incomplete specimen of *claparedii*, atypical as to the number of nephridia. He therefore merged both species under the older name of *pusilla* (Ashworth, 1912). The great majority of later writers term it *claparedii*, and Fauvel (1927) explicity rejects Ashworth's proposal, not denying the identity of the two species, but because of the inadequacy of the definition of *pusilla* and the aberration of the type specimen.

Of *claparedii*, Ashworth (1912) wrote: 'The general habits of this species, which the writer had an opportunity of observing in Naples for some weeks, are similar to those of *A. marina*. Examples taken by Prof. A. D. Howard in Puget Sound were found generally in ordinary sandy beaches, but two larger specimens were burrowing in a coarse gravelly and rocky beach.' Describing the occurrence of *claparedii* on Vancouver Island, Berkeley & Berkeley (1932) write: 'It evidently occurs over large stretches of the sand exposed at low tide at Long Bay, judging by the enormous number of casts to be found.' Takahashi (1934) describes it as living in U- or V-shaped burrows, of depth 15–25 cm., the openings 3–10 cm. apart; in certain bottoms, the burrows of *marina* may be very like this (Wells, 1945). Now *claparedii*, while resembling *marina* in its general structure, differs in two points that one would expect to be of great functional importance; it lacks statocysts, and it lacks giant nerve fibres. The similarity of its way of life to that of *marina*, which the above citations suggest, makes these differences the more surprising. The breeding habits of *claparedii* are rather different in Canada and in Japan, according to the accounts of Guberlet (1934) and Okuda (1938).

For *ecaudata*, we have the following account by Ashworth (1912): 'It occurs in the littoral zone but chiefly in sandy, gravelly or muddy material among stones, or in clefts at the base of the rocks in the debris formed by the breaking down of the latter. A considerable amount of organic matter is generally present in the material in which the worm lives. The burrows of *A. ecaudata*...are oblique or sinuous cavities, lined with a fair amount of mucus, and situated a few inches below the surface in gravel or between rocks and stones. The castings of the worm, being composed of coarse material having little coherence, soon fall apart. The well-known signs—the sand-rope-like heap of castings and the funnel-like depression in the sand—which indicate the presence of *A. marina* on countless sandy beaches, have no good counterparts in the case of the ecaudate species, in which both the castings and the mouth of the burrow are inconspicuous among their surroundings.' Fauvel (1899*a*) comments on the occurrence of *ecaudata* in black, often foetid, sandy material between rocks at Cherbourg; the galleries are more or less sinuous and often horizontal; their walls are never yellow, as those of *marina* are. The worms are found at Plymouth in just such situations as these authorities describe, and it appears that the striking differences of structure between *marina* and *ecaudata* are paralleled by equally striking differences of habit.

Methods

Preparation of worms for dissection

Ashworth (1904) recommends that lugworms should be killed with chloroform and dissected fresh, under sea water, 'as soon as possible after they are taken from the sand'. I find that formalin material, dissected within a week or

so of killing, is very much better. Fresh worms bleed easily and freely, while in formalin material the blood sets into a firm, uniform gel, so that such operations as the removal of the whole or part of a ventricle can be performed with ease. Moreover, the septa and other membranes of fresh worms are so transparent that their relations are hard to make out. The slight cloudiness which appears in formalin material is a great improvement.

The animals used in the present study were killed in either of two attitudes, 'relaxed' or 'distended'.

Relaxed worms. The worms are narcotized by immersion in a large volume of $7\frac{1}{2}\%$ $MgCl_2$. The time taken varies with the size of the worm; *marina* about 10 or 15 cm. long is fully relaxed in $3\frac{1}{2}$ or 4 hr. They are then transferred to a bath of $7\frac{1}{2}\%$ $MgCl_2$ containing 4% formaldehyde. At this stage, they may show slight movements, so it is as well to do the killing in a rectangular tank, and, if necessary, to straighten the worms against the side with a glass rod. They die in a very natural configuration. The body is straight (except for a slight ventral curvature of the first few segments). The proboscis is generally withdrawn. The worms can be stored in formalin until required. The organs usually retain quite a lot of their colour for some days, and even after months of preservation, such material is easy to dissect.

Distended worms. The worms are narcotized as above, then distended, one by one, in the following way. A cannula is connected by rubber tubing to a funnel; the whole is filled with the Mg-formalin mixture, and the tubing is closed with a screw clamp. The level of fluid in the funnel should be 15–20 cm. above the bench. The cannula is then tied into the tail, pointing forwards; it must go into the coelome, not the gut, and the way to ensure this is to insert it into an incision made in the lateral aspect of the tail. The worm is then tumbled into a long tank of the Mg-formalin mixture, and immediately distended with the same solution, by opening the screw clamp. A surprising degree of stretch is produced, and although the resulting attitude is highly unnatural, the distension straightens out the septa and other organs and greatly facilitates the study of their relationships. The proboscis is fully extruded.

Preservation for museum purposes

As many of the specimens to be found in museum collections are ill-preserved, and in very distorted attitudes, so that even their external characters are hard to make out, it may here be pointed out that worms killed in the 'relaxed' attitude, as directed above, are very suitable for museum purposes. Alcohol makes the worms rather hard, and they may easily break on handling.

Serial sections

Before sectioning, the worms were killed in Mg-formalin in the relaxed attitude, then at once transferred to Susa. The following techniques were found useful:

(i) 15 μ paraffin sections, stained with haematoxylin-eosin or Hansen's trioxyhaematin followed by Mallory's phosphomolybdic acid-aniline blue-orange G mixture, and mounted in balsam.

(ii) 100 μ celloidin sections, very lightly coloured with haematoxylin and orange G, and mounted in balsam without removal of the celloidin.

(iii) 300 μ celloidin sections, mounted unstained in glycerine jelly without removal of the celloidin.

In general, and especially when dealing with the front end of the worm, the horizontal plane is more useful than the sagittal.

Special methods

Polarized light is invaluable for working out the arrangement of the muscles. It can be used on sections, or on such objects as pieces of the body wall of distended worms, spread out flat and cleared. To avoid the necessity of turning the slide on the stage, which makes the working out of complicated muscular networks rather tricky, I have mounted two Polaroid disks, 7 in. in diameter, on a common vertical axle. One goes above, and the other below, the stage of my binocular microscope; by turning the axle, the plane of polarization of the light can be rotated without disturbing the specimen.

Spectacular preparations of the vascular system can be made by choosing unpigmented or lightly pigmented worms, distending them, then rapidly dehydrating the whole worms and clearing them in benzyl alcohol, in which they are kept.

When studying the movements of living worms, they should be placed in glass tubes; a suitable arrangement for this purpose was described elsewhere (Wells, 1945).

The Main Regions of the Body

Arenicola shows very clearly the tendency, which generally appears in sedentary polychaetes, to differentiate the chain of fundamentally similar segments, of which their body consists, into distinctively specialized regions.

The common lugworm, *A. marina*, has 19 segments with parapodia (rarely 20), and, although these segments show certain local specializations (gills restricted to segments vii–xix, nephridia restricted to iv–ix, etc.),[1] they are all built on a very evident metameric plan. These 19 segments together occupy the middle of the body and form a comparatively unspecialized region from which the two extremities stand out in marked contrast. Anterior to the first chaetigerous segment, there is a short, bluntly conical region, composed of the prostomium and one or two segments which have lost their appendages—one according to Lillie (1905), and two according to Ashworth (1904, 1912). The whole of this region is welded into a functional and structural unit, mainly in connexion with proboscis activity, and its metamerism is hard to make out.

[1] Roman numbers are used to identify particular segments.

At the hinder end of the body is the conspicuous 'tail', again composed of segments which have lost their appendages, and apparently lengthening continually backwards, in young animals at least, from reserve segments at its base (Fig. 1 A). We may therefore describe the body of *marina* as differentiated

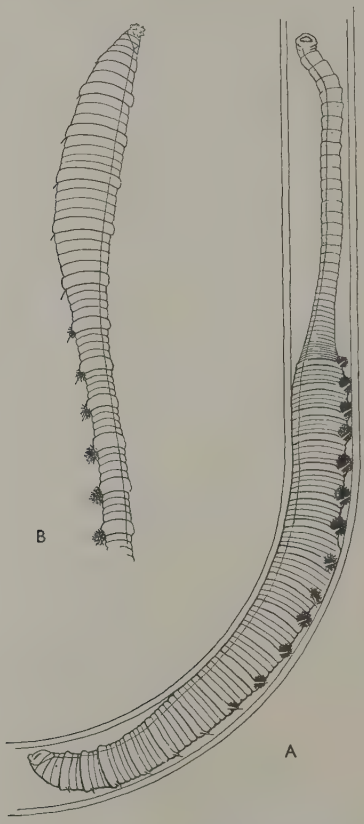

Fig. 1. *Arenicola marina*. A, a healthy individual lying, head downwards, in a glass observation tube. Most of the chaetigerous segments are pressed, laterally and ventrally, against the walls of the tube, but are separated from it by a narrow space on the dorsal side. Waves of swelling, which occlude this space, are travelling gently headwards and so driving water through the tube; one such wave is passing the 5th and 6th gills. B, the 'clubbed' attitude, which often appears in moribund specimens.

into three very distinct regions—an achaetous anterior region, or 'head', a chaetigerous middle region, or 'trunk', and an achaetous posterior region or 'tail'. The middle region shows various subsidiary differentiations, with

regard to the distribution of gills, nephridia, etc., among its component segments.

The body of *claparedii* resembles, in all the above respects, that of *marina*. In *ecaudata*, the differentiation between 'head' and 'trunk' occurs as in the other species, but the specialized third region appears, at first sight, to be lacking. The worm has a great number of segments and the parapodia and gills continue as far as, or nearly as far as, the hinder extremity. There are, however, indications of a differentiation corresponding to, though less profound than, that between 'trunk' and 'tail' in the other species (p. 37).

The above method of describing the regional organization of *Arenicola* differs from that generally adopted in the literature. Audouin & Milne Edwards (1834) wrote of *marina* as 'composé de trois portions assez distinctes: l'une antérieure, ordinairement renflée et ne portant pas de branchies, une moyenne, étroite et branchifère, et une postérieure, apode'. The anterior region, in this account, includes the 'head' and the first six chaetigerous segments. The majority of subsequent writers, down to the present day, have adopted this method of subdividing the worm. Ashworth (1904) instructs his students to 'note the shape of the worm; its division into an anterior abranchiate chaetigerous portion, middle branchiate chaetigerous region and posterior achaetous and abranchiate tail'. Fauvel (1927) describes *marina* thus: 'Région antérieure à 6 segments uncinigères abranches. Région abdominale a 13 sétigères, branchifères. Région caudale achète et abranche de longueur variable, fragile.' The gills have also been used to characterize the regions of *ecaudata*. 'Le corps', wrote Fauvel (1899*a*) of this species, 'se divise en deux parties: 1° la région anterieure ou thoracique qui comprend le prostomium, le segment buccal, un segment post-buccal achète et 15 ou 16 segments pourvus de parapodes et de tores uncinigères mais abranches; 2° la région abdominale dont tous les segments portent des parapodes et des branchies sauf parfois les 1 à 7 derniers qui sont abranches mais toujours sétigères.'

It seems to the writer, that the method of subdividing the body with reference to the gills is rather misleading. Of the various divergent specializations which differentiate the segments of *Arenicola* from each other, some are extremely constant and fixed in position, not only from individual to individual but also from species to species. Such, for example, are the persistence of septa i, iii and iv of the middle region as the well-known 'diaphragms', or the elaboration of the vessels of the (vanished) septum vii to form the ventricles, closely applied to the gut and separating its oesophageal from its gastric part. Others, on the other hand, fluctuate; for example, the nephridia are always restricted to a limited number of segments, but the number and position along the body of the segments concerned varies, not only from species to species but also to some extent from individual to individual. When seeking for criteria of regional differentiation, one should clearly choose characters of the former kind; yet the distribution of the gills, which so many

authorities use, is of the latter. In the 'caudate' species, i.e. in all those with an achaetous 'tail', the most anterior gill is typically on segment vii, and the division between abranchiate and branchiate regions therefore coincides with the position of the hearts and boundary between oesophagus and stomach. In the so-called 'ecaudate' species (*ecaudata* and *grubii*), the most anterior gill lies several segments farther back, though the cardiac and enteric differentiations remain at the same level as before. Even in the caudate species, including *marina*, 'the first gill is almost invariably small, and in a considerable percentage of examples, is reduced to minute proportions or is absent' (Ashworth, 1912). The same is true of *ecaudata*. Evidently, the boundary between abranchiate and branchiate regions is by no means a rigidly fixed one, and when more constant intersegmental differentiations are available, there is no justification for subdividing the body on the basis of the distribution of the gills. The division into 'head', 'trunk' and 'tail', described above, is undoubtedly the most profound of the local specializations exhibited by *Arenicola*, and is merely obscured by throwing together the 'head' and the first few 'trunk' segments into an 'anterior abranchiate chaetigerous portion'.

In conclusion, a word may be said about the 'renflée' and 'étroite' of Audouin & Milne Edwards' description, cited above. One sometimes finds lugworms in which the first half a dozen or so segments are distended and the rest of the trunk is narrowed by contraction of the circular muscles. The worm as a whole is therefore club-shaped (Fig. 1 B). One never sees this attitude in vigorous, healthy worms, but only in dead or moribund specimens. It is very common in worms which have been badly collected, for example, in a hot, overcrowded jar. I believe its assumption to be an irreversible process, and a sign of approaching death; if any of the worms in my stock tanks exhibit it, they are thrown away before they die and foul the water.

The point would be hardly worth mentioning, were it not that 'clubbed' worms have appeared very often in the literature. The 'renflée' and 'étroite' in Audouin & Milne Edwards's description, together with their Pl. 8, fig. 8, show unmistakably that their worms were in the 'clubbed' attitude. Grube (1851) also refers to the anterior part of the body as 'mehr oder minder aufgebläht'. More recently, a beautifully drawn figure of a 'clubbed' worm was published by Cunningham & Ramage (1888) and reproduced in the well-known *Handbuch* of Kükenthal-Krumbach (Hempelmann, 1934, p. 191). A striking example is to be found in the *Cambridge Natural History* (Benham, 1896, p. 333). In healthy worms, however, or in those prepared by the Mg-formalin method, no trace of 'clubbing' can be seen. When we bear in mind, first, that the part of the body which distends in this abnormal attitude is also the pre-cardiac or 'anterior abranchiate' part, and, secondly, that many of the early authorities based their descriptions on specimens thus distorted, we may infer that the 'clubbed' attitude has some responsibility,

historically, for the idea that the boundary between abranchiate and branchiate regions represents a differentiation of major importance.

The Body Wall and Appendages

The account of the body wall follows the division of the body as a whole into three regions, as explained in the last section. The general plan of the body wall, common to all the regions, will be described first.

THE GENERAL STRUCTURE OF THE BODY WALL

The body wall is divided externally into *annuli*, separated by *interannular grooves*. The position of the nerve cord is marked externally by a conspicuous, pale *ventral groove*, in *marina* and *claparedii* but not in *ecaudata*.

The body wall consists of the following layers: (i) epidermis, (ii) subepidermal connective tissue, (iii) circular muscle, (iv) a layer of intermuscular connective tissue, which is brought out prominently by the aniline blue of Mallory's triple stain, (v) longitudinal muscle, (vi) coelomic epithelium. A series of oblique muscles, of the usual polychaete type, is generally present (Fig. 2). The body wall is richly vascularized, and one can generally see in sections that the blood vessels lie in tubular spaces; these are extensions of the coelome, penetrating into the body wall.

The *circular muscle layer* is interrupted by a radial partition of connective tissue at each interannular groove (Fig. 5C–E, p. 17). According to Lillie (1905), the circular muscles develop very much later than the longitudinal in *A. cristata* Stimpson—a species very similar to *marina*.

If one takes a piece of body wall from a distended specimen, clears it, spreads it flat on a slide, and then examines it between crossed polaroids, rotating the slide relative to the plane of polarization, one finds that the whole of the musculature at any given point on the body wall, both circular and longitudinal, blacks out in the same position. This means that the musculature of the general body surface consists *only* of these two series of fibres, whose molecules are orientated truly at right angles to each other. There can be no diagonal or spirally running fibres, as occur, for example, in several Oligochaeta.

The fibres of the *longitudinal layer* are grouped, in *marina* and *claparedii*, into a great number of longitudinal columns, each covered by coelomic epithelium. These columns branch and anastomose with their neighbours, and form a conspicuous and characteristic background when one dissects either of these species (Fig. 3A–C). In *ecaudata*, on the other hand, the body wall presents a smooth appearance internally; the longitudinal layer is covered over by a continuous peritoneal sheet which is only occasionally perforated or grooved to accommodate a blood vessel (Fig. 3D).

In all species, certain *lines of separation* can be traced in the longitudinal layer, which are important anatomical landmarks. They are usually evident in

dissections, and are especially obvious in distended material. They appear, in *ecaudata*, as longitudinal clefts in the layer, and in *marina* and *claparedii* as deep grooves between adjacent muscle columns, across which anastomoses seldom or never occur. The lines are (Fig. 2): (i) the *ventral line*, in which the nerve cord (*n.c.*) lies; (ii) the *nephridial lines* (*neph.l.*), at the level of the nephridiopores; (iii) the *notopodial lines*, (*notop.l.*), through which the inner ends of the notopodia protrude into the body cavity; and (iv) the *dorsal line*

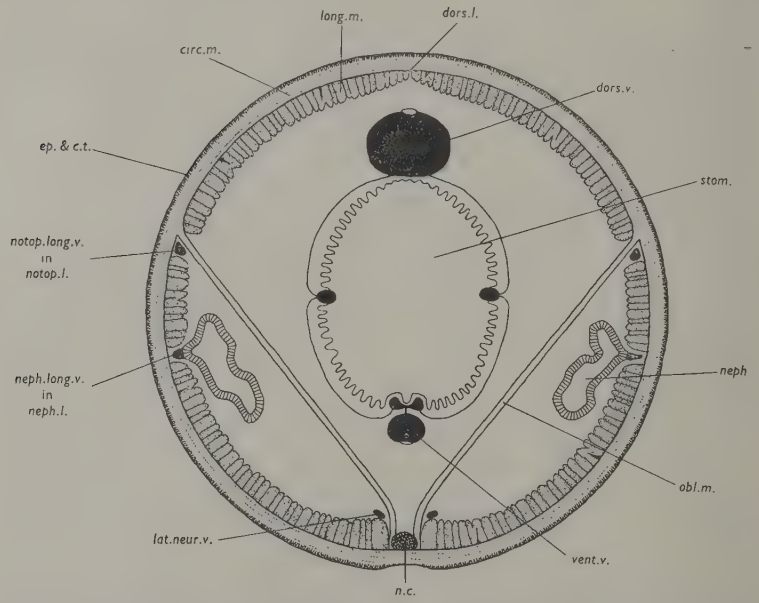

Fig. 2. *Arenicola marina*. Transverse section of an ordinary annulus, drawn from a section slightly anterior to the eighth chaetigerous annulus. For explanation of the lettering on the figures, see list on p. 44.

(*dors.l.*), into which the dorsal mesentery, where present, is inserted. The ventral, notopodial and dorsal lines are always present, and may perhaps divide the longitudinal musculature into functionally distinct fields. The nephridial lines are more variable; they are evident along the whole length of *ecaudata*, and in the trunk, but not the tail, of *marina*. In *claparedii*, they can be made out only in the immediate neighbourhood of the nephridia.

The *ventral nerve cord* is rounded in section and without segmental enlargements. It gives off a pair of interannular nerves in each interannular groove; these nerves run round the body to unite dorsally and so form a hoop enclosing

the body. They lie in the connective tissue partitions which divide the circular muscle layers in the interannular grooves (Fig. 5C–E, *interann.n.*). There is also a special outflow of nerves in each chaetigerous annulus, details of which have not yet been traced. The cord itself consists of a deep (dorsal) fibrous part and a superficial (ventral) ganglionic part. A giant fibre system is present in *marina* and *ecaudata*, but not in *claparedii*. Details of the giant fibre system

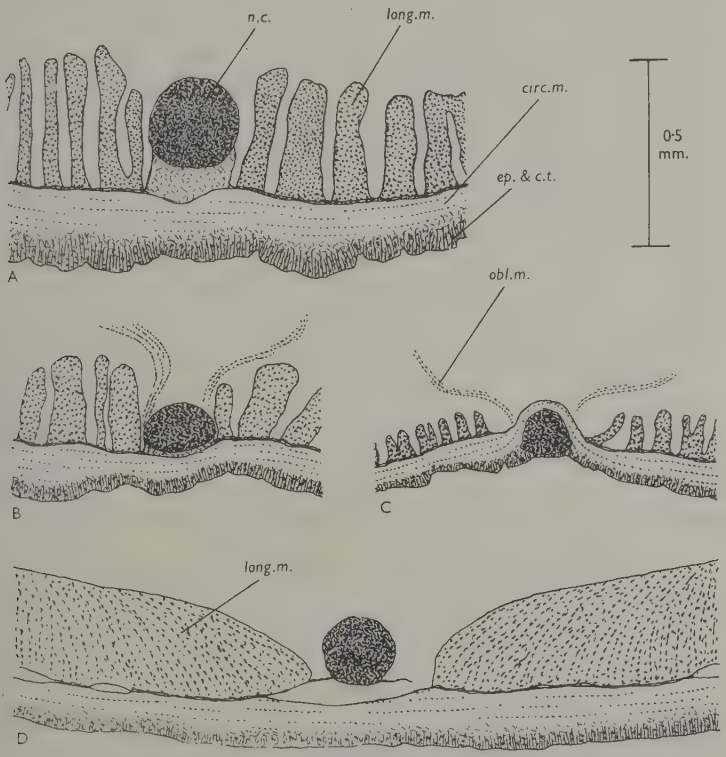

Fig. 3. Transverse sections through the body wall of ordinary annuli, in the region of the ventral nerve cord. A, *marina*, segment iii; B, *marina*, segment xviii; C, *claparedii*, segment xiv; D, *ecaudata*, segment xii. Lettering as on p. 44.

are given by Gamble & Ashworth (1898, 1900), by Ashworth (1904) and by Nicol (1948).

The position of the nerve cord relative to the layers of the body wall varies from species to species. The most primitive condition is presumably that found in *claparedii*, where it lies superficial to the circular muscle layer and in intimate relation with the epidermis (Fig. 3C). In the other two species, the

cord lies deep to the circular muscle layer.[1] In *marina*, it is separated from the circular layer by a pad of connective tissue, staining conspicuously blue with the aniline blue in Mallory's triple stain, and thicker in the anterior segments of the body than farther back (Fig. 3 A, B). In *ecaudata*, this pad is absent, and an extensive coelomic space separates the cord from the circular muscle (Fig. 3 D). The cord is held in position by a membranous sheet running laterally to the longitudinal muscle layer, and perforated in many places to allow blood vessels to pass. The peripheral nerves reach the body wall by way of this membranous sheet.

The *oblique muscles* have the form of flat, translucent strips. They run from the sides of the nerve cord to the notopodial line, where their fibres enter, and join, the circular muscle layer. Particularly thin, thread-like members of the oblique muscle series are attached to the inner ends of most of the notopodia. Oblique muscles are absent from the heads of all species, and (except for those attached to the notopodia) from the first 3 trunk segments of *marina* and *claparedii* and the first 16 or 17 of *ecaudata*. Thereafter they continue to the hinder extremity of the body.

There is of course no jointed skeleton, and the main skeletal function is presumably performed by the body fluid. The pressure in the coelome has been measured in *marina* under various conditions by Chapman & Newell (1947); they find that it increases with the level of activity of the worms and, in actively burrowing individuals, may exceed 30 cm. of sea water. We may suppose that in active animals, both layers are in a state of sustained tonic contraction, and that the changes of form are produced by local increases, or local decreases, in the tensions of the two layers.

The following considerations suggest that the circular layer plays the greater part in the postural function of maintaining internal pressure. Suppose a cylindrical worm whose length is great and the thickness of whose body wall is small compared with its radius r cm. Let the pressure in its body fluid be P g. wt./cm.^{2}, and let it be entirely due to the tensions in the circular and longitudinal layers, which, as with surface tension, we call S_C, S_L g. wt. cm.

Now imagine a plane dividing the worm transversely. If no change of shape is taking place, the hydrostatic pressure acting over the area of section is balanced by the longitudinal muscle tension round the circumference, and we have

$$\pi r^2 P = 2\pi r S_L \quad \text{or} \quad S_L = \tfrac{1}{2} P r. \tag{i}$$

[1] Ashworth (1904) writes of *marina*: 'In some specimens the cord in the tail and in the last chaetigerous segment lies only just below the epidermis.' I find, on examining serial sections of the tails of seven worms, that the cord lies deep to the circular muscles in all but one. In the single exception, the cord seems in some sections to lie as in *claparedii* while in others it is embraced by the circular muscle, the latter running both superficial and deep to it. This is much the smallest worm of the seven (tail diameter 1·1 mm.) so the appearances may represent a migration during development from the primitive to the final position. This specimen has the cord deep to the circular muscle in the chaetigerous segments.

Now imagine the worm divided by a longitudinal plane passing through its long axis. This time, the pressure is balanced by the circular muscles, and, if the length is l cm., we have

$$2rlP = 2lS_C \quad \text{or} \quad S_C = Pr. \tag{ii}$$

Combining (i) and (ii)

$$S_C = 2S_L. \tag{iii}$$

How far do these considerations apply to a real *Arenicola*? In the first place, the muscle layers have a measurable thickness; this is, however, not great compared with the radius and its effect will be to apply a small correction to the quotient 2 in equation (iii). Secondly, the oblique muscles may have a postural function; they are, however, very thin, and absent from a fairly considerable stretch of the body in *ecaudata*; and we may note, in passing, that septa and mesenteries are lacking over most of the trunk in all species. Thirdly, the body fluid is not the only skeleton. Isolated branchiate segments of *marina*, lying in a watch-glass of sea water, often undergo regularly rhythmical changes of shape, not perhaps very extensive but perfectly visible and corresponding in timing with the waves that traverse the body, when water is being pumped through the tube. This observation shows that there is a certain amount of elasticity in the body wall itself, though it seems probable that this factor plays only a minor role in the intact worm. Finally, there is the skeletal function of the surrounding mud. The movements of *marina* in glass tubes have been studied by various authors (Just, 1924; van Dam, 1937, 1938; Wells, 1944, 1945), and will be treated in a later section. For the present, we need only note that there appears to be an inverse relation between the degree of activity of the worm and the proportion of its surface which makes contact with the tube. At one extreme, it may be completely at rest: in this posture, the body is short and thick and presses against the tube with its whole surface; thus the relationships discussed above obviously do not apply. At the other, it is creeping actively forwards or backwards: the body is extremely elongated and at all points away from the tube, except that waves of swelling run along it, grip the tube, and so act as fixed points; here, as the waves follow each other fairly rapidly, the trouble lies in the assumption that no change of shape is taking place.

Evidently, equation (iii) is not to be taken as precise. It may, nevertheless, point in the right direction. Lugworms kept in glass tubes often show a regular alternation of rest and rhythmic activity. The resting worms are short and thick, and the onset of an activity outburst is accompanied by lengthening and narrowing of the body (Wells, 1949*a*). Spontaneous activity is also associated with an increase in internal pressure (Chapman & Newell, 1947). The phasic responses to stimulation are suggestive in this connexion. A nocuous stimulus may produce sudden shortening of the head or tail, or curving of the body (Just, 1924)—results evidently due, in the main, to

longitudinal muscle contraction. If a worm is creeping into a tube, and an attempt is made to pull it out backwards, it expands its front end very abruptly to grip the tube, a movement which suggests circular muscle inhibition. The data as a whole suggest that, in an active worm, the circular muscles are fairly highly contracted and the longitudinals less so; the phasic acts, whether reflexly or spontaneously produced, are mainly, at least, in the sense of longitudinal contraction and circular inhibition.

Fox (1949) has pointed out that the muscles of *Arenicola* contain haemoglobin, but does not discuss whether there is any inequality of distribution between the muscle layers. For the other pigments of the body wall, the works of Fauvel (1899*b*) and Lignac (1945) may be consulted.

The epidermis is richly provided with unicellular gland cells. The skin secretes mucus, which is used, in *marina*, to impregnate the wall of the burrow and keep it firm (Osler, 1826; Linke, 1939). The mucus of *ecaudata* is particularly copious, as anyone who has handled the living worm is aware. If specimens of *marina* are kept in the laboratory, the water comes to contain 'belts' of greyish mucus, of about the same diameter as the worms; these belts are sometimes seen round their bodies; they appear to be passed slowly headwards and to be a means of getting rid of such unwanted residues as the breakdown products of old chaetae. When handled, the lugworm produces a fluorescent, greenish yellow secretion, which stains the fingers and is also rather irritating.[1]

THE MIDDLE REGION ('TRUNK')

As the middle region of the body is in many ways the least specialized of the three, it will be taken first.

Arenicola marina

The trunk of this species consists of 19 segments (in exceptional individuals, 20). They exhibit a certain amount of structural and functional divergence. Each segment includes several annuli, of which one, the *chaetigerous annulus*, is larger than the others and bears the parapodia and gills. The chaetigerous annuli are shown white in Fig. 4. The boundaries between segments are given internally by septa, or, where the septa have disappeared, by the septal blood vessels. The septal planes correspond approximately, though not quite exactly, to the second groove behind each chaetigerous annulus: in other words, the penultimate annulus of each segment is chaetigerous.

Typically, any two chaetigerous annuli are separated by 4 ordinary annuli, so that the number of annuli per segment is 5. In the first 3 segments, however, the number of annuli is reduced. The first has 2, the second 3 and the third 4, except that in a 'laminarian variety', described by Gamble & Ashworth (1898), the third has 3. The fourth, and all subsequent trunk

[1] The worm as a whole has a characteristic fragrance, especially when laid open. After he had worked on it for some years, it produced strong allergic symptoms in the writer (catarrh, asthma); this was put right by a course of injections.

segments, have 5 each. The rule, that the chaetigerous annulus is penultimate, holds for the anterior segments in spite of this reduction.

Ashworth gives no attention to the possible systematic usefulness of these numbers. It is true of all *Arenicola* species, that the majority of the trunk segments have 5 annuli, and that some degree of reduction occurs at the front

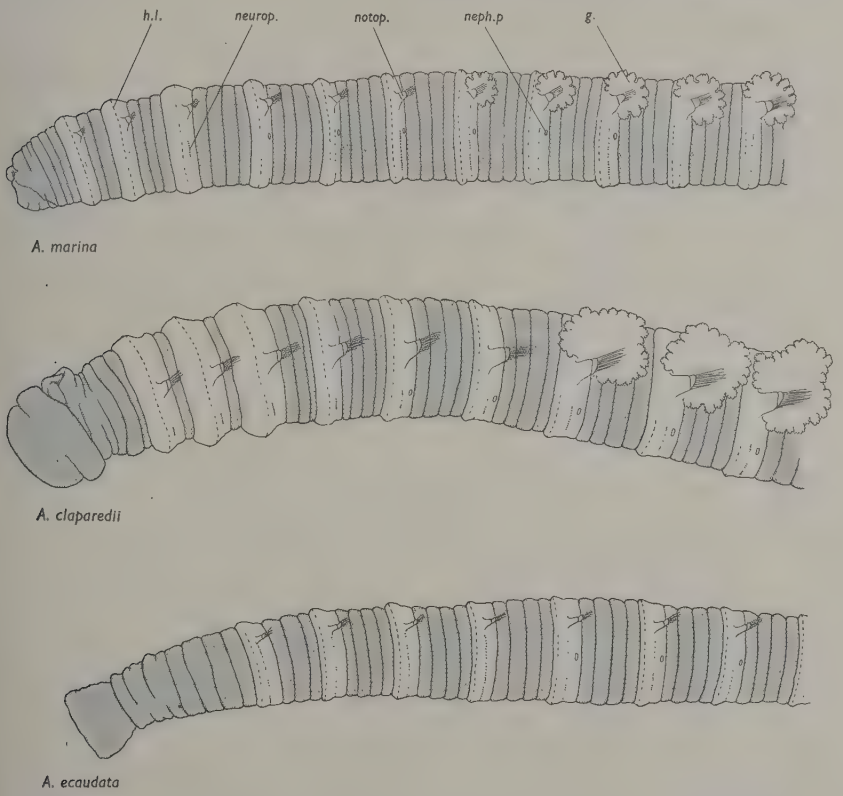

Fig. 4. Lateral views of the front ends of the three species, to show the annulation and the characters of the chaetigerous annuli and appendages (white). The proboscis is withdrawn in the *marina* and extended in the other two. Lettering as on p. 44.

end. The extent of this reduction is not always the same, and I find that each of the species now under examination has a fairly constant and characteristic annulation formula, which holds for all the range of material which I have been able to examine (p. 2).

The most convenient way of describing the reduction is to use serial Roman figures for the chaetigerous annuli, and to put between them, in Arabic

figures, the numbers of intervening ordinary annuli. Thus the typical formula for *marina* is:

i.2.ii.3.iii.4.iv.4.v ...

While the 'laminarian variety' is:

i.2.ii.2.iii.4.iv.4.v ...

The structure of the ordinary annuli has already been sufficiently described. We turn now to the distinctive features of the chaetigerous annuli. These are: (i) the neuropodia, (ii) the notopodia, (iii) the parapodial girdles, (iv) the gills, and (v) the nephridia and nephridiopores.

The earlier authorities were mainly interested in the characters supposed to be of systematic importance—the detailed form of the chaetae, and the mode of branching of the gill. Full information about these points is to be found in the works of Gamble & Ashworth (1900) and Ashworth (1912). The musculature and functional topography of the appendages were described, for *marina* only, by myself (Wells, 1944). The main results for that species will now be summarized.

A *neuropodium* consists essentially of a single dorsi-ventral row of chaetae, each with a sharply inclined rostrum projecting from the body surface and a gently curved shaft embedded in the body wall (Fig. 5A, B). Each chaeta lies in its own epithelial follicle. The whole row of chaetae and follicles may be termed the neuropodial plate. New chaetae and follicles are continually being formed in a highly basophil formative region (Fig. 5A, *form.*) at the ventral end of the plate, and old ones are destroyed at the dorsal end, where their products accumulate as greenish masses (*dest.*). These are somehow expelled from time to time. There therefore appears to be a continual dorsalwards procession of chaetae and their follicles along the neuropodial plate.

To see the musculature of the neuropodium, longitudinal sections, cut at right angles to the body surface, should be studied (Fig. 5C). The inner end of the neuropodium projects into a cavity, cut off from the general coelome by the longitudinal muscle layer. Retractor muscles run from the longitudinal layer to the outer edge of the neuropodial plate (*ret.m.neurop.*), and protractors run anteriorly and posteriorly from its inner edge to the neighbouring body wall (*prot.m.neurop.*).

The neuropodia of the more anterior segments are very short dorsi-ventrally, but they lengthen from segment to segment until, from segment x or xi backwards, they extend from a point slightly above the nephridial line to the side of the nerve cord (Fig. 4).

I know of no published description of the movements of the neuropodial chaetae. They could obviously be protracted to some extent by the protractors, and withdrawn again by the retractors, if the substance of the annulus is sufficiently flexible. I am, however, inclined to guess that another movement is more significant. Simultaneous contraction of the posterior protractors and

anterior retractors would tend to incline the chaeta as a whole, so that its inner end would move backwards relative to its outer; at the same time, owing to the form of the chaeta and the position in which it normally lies in the neuropodial plate, it would rotate so that the rostrum points forwards (Fig. 5 A, B). Similarly, the anterior protractors and posterior retractors could turn the rostra backwards. The usefulness of this movement, in facilitating the ratchet or gripping function of the neuropodia when the worm is creeping along the tube, needs hardly to be stressed.

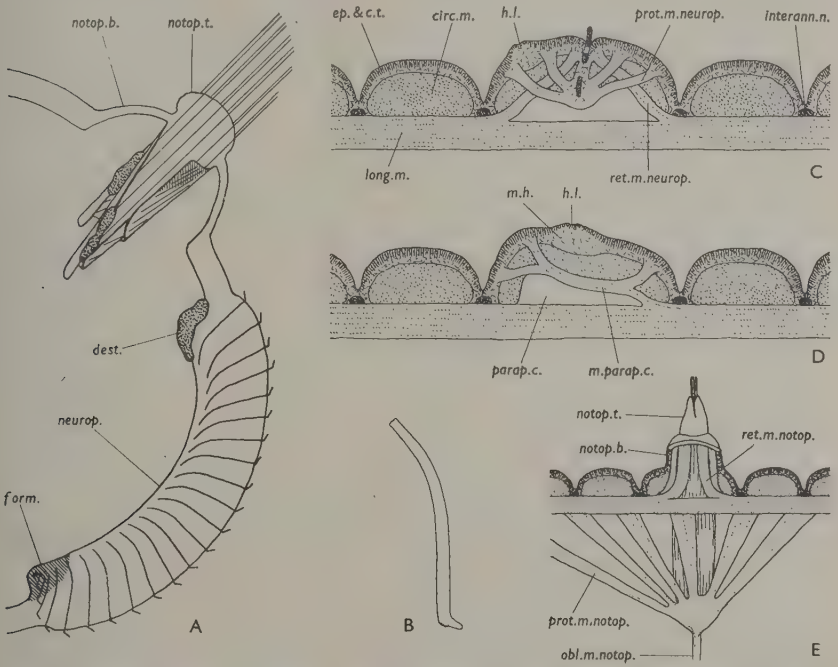

Fig. 5. *Arenicola marina*. Diagrams of the parapodia. A, the essential structure of a notopodium (above) and a neuropodium (below). B, a neuropodial chaeta. C, longitudinal section through one of the hinder neuropodia, at right angles to the body surface. Two ordinary annuli are also included. D, sagittal section through one of the first three chaetigerous annuli, near the mid-dorsal line. E, the muscles of a notopodium, exposed by a longitudinal cut through the body wall passing through its base. Lettering as on p. 44.

A *notopodium* can be regarded as a modified neuropodium. In external view, a dorsi-ventrally flattened tip (Fig. 5 A, E, *notop.t.*) can be distinguished from a thin-walled, evaginable base (*notop.b.*). The chaetae are very long and emerge from the tip in two closely applied, parallel rows. To derive a notopodium from a neuropodium, the plate must be supposed to have duplicated itself into two plates lying close side by side like two leaves of a book, and then the inner

corners of the double plate to have been folded and rolled forwards, giving the inner end of the whole a somewhat scroll-like appearance (Fig. 5A). The resulting structure is complicated and not easy to visualize. Full details of the notopodium and its musculature were given elsewhere (Wells, 1944).

The inner end of the notopodium protrudes through the longitudinal muscle layer into the general body cavity. The protractor muscles radiate from this end to the surrounding body wall (Fig. 5E, *prot.m.notop.*). Most of these run anteriorly and posteriorly, but one or two are inserted on the body wall dorsal to the notopodium, close to its base, while others spread ventrally as far as the nephridial line (Fig. 6). A thin strand of muscle generally runs from the inner end of the notopodium to the side of the nerve cord, and this has often been described as the retractor of the notopodium. It is evidently a member of the oblique muscle series; and, as it is quite often absent, we cannot suppose that it plays an essential role in the movements of the podium. (Fig. 5E, *obl.m.notop.*). The true retractors resemble those of the neuropodium; they run from the longitudinal muscle layer to the notopodial tip (Fig. 5E, *ret.m.notop.*). There are also thin sheets of muscle sheathing the notopodial plates, and running between their inner ends.

The notopodia further resemble the neuropodia in that they are smallest in the more anterior segments, and increase gradually in size posteriorly.

A notopodium is connected to the general body wall only by the muscles and the thin-walled, invaginable base. It must therefore be held in position by its muscles, contracting tonically against each other. If a living worm is watched under a binocular microscope, two types of movement of the notopodium can very readily be seen. The first is retraction and protraction, i.e. invagination or evagination of the base, and the second is the direction of the tip in an anterior or a posterior direction. We may conjecture that invagination is brought about by the retractors, with the possible assistance of the oblique muscle of the notopodium, evagination by the protractors, anterior pointing by the anterior retractors and posterior protractors, and backward pointing by the posterior retractors and anterior protractors. A high pressure of the body fluid will tend towards evagination. From the arrangement of the muscles, it would also be possible to swing the tip dorsally and ventrally, and perhaps to rotate the podium on its own long axis, but I am not aware that such movements have been witnessed or described.

The *parapodial girdle* is a name now proposed to cover a group of special features of the chaetigerous annulus to which I drew attention elsewhere (Wells, 1944). These features are best seen in a sagittal section through one of the first three segments, somewhere near the dorsal line (Fig. 5D). The chaetigerous annulus stands out at once in such a section, because it contains a conspicuous cavity, the 'parapodial canal' (*parap.c.*). This canal runs right round the annulus, and is separated from the general body cavity by the

longitudinal muscle columns, and by a connective tissue sheet on which they rest. It communicates with the general cavity only at the notopodial, nephridial and ventral lines (Fig. 6). Outside the parapodial canal is a special longitudinally directed musculature, arching in the main from the front to the rear half of the annulus, but also running into the longitudinal layer posteriorly ('muscles of the parapodial canal', Fig. 5D, *m.parap.c.*). If now one looks at the surface of one of these annuli, one sees that it is girdled by a pale line, usually elevated as a slight ridge (Fig. 4, *h.l.*); this is the 'hinge line' and under it, in the subepidermal connective tissue, a series of fine, antero-posteriorly running muscles can be detected ('muscles of the hinge', *m.h.*). All of these structures run right round the annulus, except only for the ventral line, where it is crossed by the ventral groove.

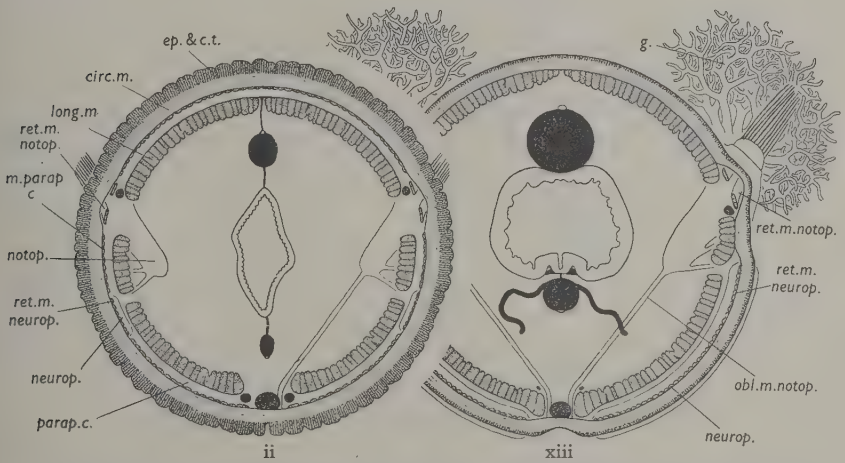

Fig. 6. *Arenicola marina*. Transverse section through chaetigerous annuli ii and xiii. The worm was transected in front of the appendages, and drawn with a binocular: the appendages are therefore seen just beyond the plane of section. Compare Fig. 2. Lettering as on p. 44.

We have already seen that the neuropodia and notopodia are small in the more anterior segments, and increase in size as one passes backwards. Just the opposite is true of the parapodial girdle (Fig. 4). The hinge line approaches more and more closely to the front of the annulus in segments iv–viii, and at the same time the parapodial canal and the two special musculatures decrease in importance and move with it. At first sight, each of these chaetigerous annuli looks rather like two; the front part is raised and swollen by the parapodial girdle, while the hinder part is flatter, like the rest of the body wall. Finally, from segment ix onwards, the parapodial girdle disappears altogether from the dorsal part of the annulus.

Now, on comparing C, D and E in Fig. 5, it will be seen that there is a considerable degree of resemblance between the musculatures of the notopodium, of the neuropodium, and of the parapodial canal. The two former can be regarded as derived, in part at least, from the latter. The cavity in which the inner end of the neuropodium lies is clearly a part of the parapodial canal (Fig. 6), and by analogy the invaginable notopodial base can also be so derived. In other words, the parapodial girdle persists in the hinder segments, but only in connexion with the notopodia and neuropodia. The hinge line can be seen, running down the front of the neuropodium, on many of the hinder segments, but it fades as one passes back, and is usually quite invisible on the last four or five.

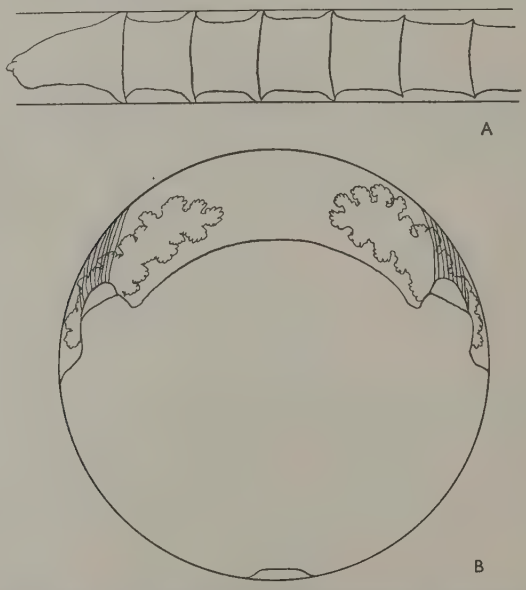

Fig. 7. *Arenicola marina*. A, the elevation of the anterior chaetigerous annuli. B, diagrammatic section of a worm circulating water through a tube, as in Fig. 1A.

There is no doubt at all about the importance of the parapodial girdle of the more anterior segments as a motor apparatus. If a *marina* is put into a large funnel of sea water, with the lower end of the stem closed with rubber tubing and a clamp, the worm usually burrows down into the stem, and the movements of the more anterior chaetigerous annuli can then be watched. At one moment they lie flat; then they are suddenly raised, and apparently distended, into the form of sharp, backwardly directed flanges; then they drop again (Fig. 7A). The whole apparatus seems to act as a single unit, i.e. all of the 'parapodialized'

annuli, and the whole periphery of any one of them, rising and falling together, though the movements are most evident in the first three segments, in which the responsible structures are best developed. The movements are used in burrowing, to grip the sand and help to draw the worm in, and also, apparently, for certain other purposes, such as the drawing of surface sand down into the head end of the burrow (Wells, 1944).

The *gills* are hollow, branched, contractile outgrowths of the body wall, borne by the chaetigerous annuli just behind the notopodia, and present on every segment from vii onwards (Fig. 4). The most anterior gill is smaller than the rest and may be lacking altogether on one or both sides. For details of the mode of branching of the gills, the works of Ashworth (1904, 1912) may be consulted.

The sphinctered *nephridiopores* open just behind, and very slightly below, the upper ends of the neuropodia, on segments iv to ix inclusive. According to Goodrich (1946) the 'nephridium' of *Arenicola* is a nephromixium and includes an ectodermal component which should logically be described with the rest of the body wall; it will, however, be included with the internal anatomy, which the writer hopes to describe in a later paper.

We turn now from the various components of which the body wall of the trunk consists, to the plan of the region as a whole. It can be divided, on structural grounds, into the following three sections (Fig. 4):

(i) Segments i, ii, iii. Gills absent. Neuropodia and notopodia small and apparently unimportant. Parapodial girdles massively developed round the whole circumference of the chaetigerous annuli.

(ii) Segments iv to viii. Graded, transitional.

(iii) Segments ix onwards. Gills present. Neuropodia and notopodia well developed. Parapodial girdle absent, except in connexion with the neuropodia and notopodia.

Now this structural differentiation is very nicely paralleled by a physiological one. The movements of *marina* were first studied in detail by Just (1924), who pointed out that the first three or four segments (the boundary is not absolutely sharp) stand in functional contrast to the rest. His observations have been confirmed and extended by others (van Dam, 1937, 1938; Wells, 1944, 1945). In burrowing, in forwards or backwards creeping, and in the driving of water through the burrow, waves of swelling travel along the trunk. These waves may go in either direction and their form varies with the particular type of movement that is being carried out. At all times, however, they concern the hinder 15 or 16 segments, and (though the amount of worm they involve varies to some extent with the type and vigour of the movement) they are seldom, if ever, shown by the first three. Proboscis activity, on the other hand, is brought about by the integrated action of the proboscis itself, of the body wall of the head, and of the body wall of the first three trunk segments.

If a worm is watched quietly pumping water through a glass tube (Fig. 1), the ventro-lateral surfaces may be noticed, over most of the trunk, to be pressed tight against the tube; a space remains, however, between the dorsal surface and the tube, and the gills spread out into this space. Waves of swelling travel along the dorsal surface, occluding the space and so driving water through the tube; the gills contract as the waves approach and expand again as soon as they pass. A rather conjectural cross-section of a worm in the act of irrigation, based on watching worms in glass tubes from the side, is drawn in Fig. 7B. The problem at once arises, of how the close pressing of the flanks against the tube is achieved. The only possible answer, I think, is by means of the notopodial protractors. It will be seen from the drawing, that the contact could be maintained if the notopodia were pressing outwards and upwards. Meanwhile, the head and first few segments (which are not concerned in the irrigation waves, and in which the notopodia are poorly developed) arch away from the side of the tube (Fig. 1).

In active creeping, as Just (1924) described, the notopodia exert a ratchet action, being directed backwards for headward locomotion, and forwards for tailward locomotion. We may fairly safely guess that the neuropodial rostra play a similar role. When swimming, the worm travels tail first, with lateral waves of great amplitude travelling headwards along the body, while the notopodia are directed headwards and held close to the body surface. The podia are never used as oars or paddles, or even as punt poles; they are bracing and anti-slip devices.

It seems, then, that the neuropodia and notopodia are adapted to assist in those wave movements which are the concern of the hinder segments, and it is in those segments that they are best developed. The first few trunk segments are specialized, partly to help in the extrusion of the proboscis by driving their contained body fluid forwards (Just, 1924) and partly for the flanging movement described above. The great development of the parapodial girdles which the latter function involves appears to carry with it a reduction in the size of the neuropodia and notopodia, and the disappearance of the gills. It is indeed striking, in a view of the whole worm, that the gills appear just as the parapodial girdles leave the dorsal faces of the chaetigerous annuli (Fig. 4).

Arenicola claparedii.

The general organization of the body wall of the trunk is the same in the other two species as in *marina*; it is therefore only necessary to note divergences.

An immediately obvious feature of *claparedii* is the enormous development of the first three chaetigerous annuli (Fig. 4). In the living worm, the movements of these annuli are like those of *marina* in type, but very much more powerful and impressive. The anatomical features which distinguish these annuli are correspondingly well developed. At the same time, this expansion has entailed

a great reduction in the ordinary annuli of the anterior segments. I find the following formula, in my Neapolitan specimens:

i.1.ii.1.iii.3.iv.4.v ...

The hindmost of the 3 annuli between iii and iv is generally much smaller than the others. Some of the American specimens at the British Museum have a second annulus between ii and iii; it is however always very small and may

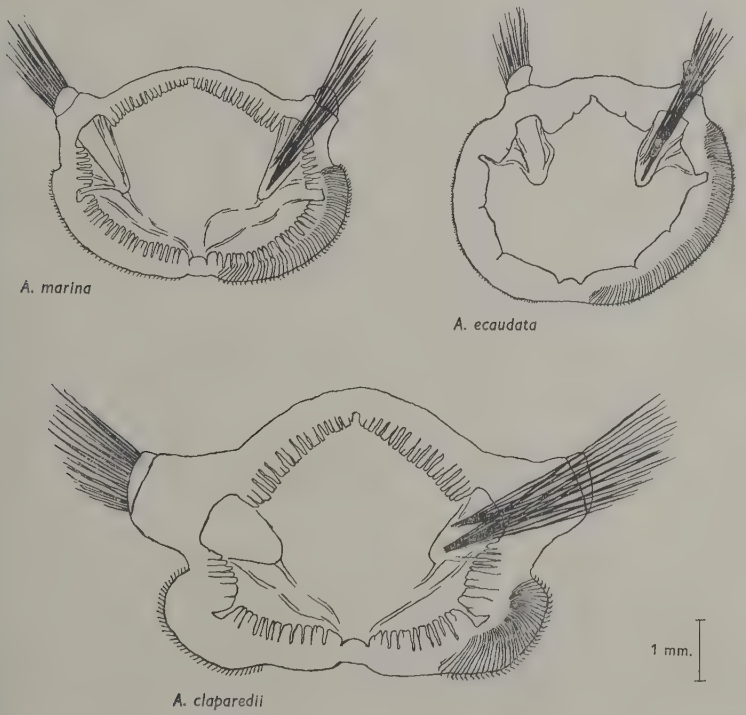

Fig. 8. Drawings, all to the same scale, of chaetigerous annulus xvi in each of the three species. Drawn from cleared specimens of the isolated annuli. The full extent of the chaetae is shown on the right, the projecting portions only on the left.

not extend round the whole circumference of the worm. In others, chaetigerous annulus iii hangs forwards in such a way that a minute ring might be present but hidden. We seem to be concerned here with an annulus in process of disappearance; and the variations described below for *ecaudata* support the idea that it is always immediately in front of the chaetigerous annuli that reduction occurs.

In a posterior direction the parapodial girdle is seen to leave the dorsal surface after segment vi—so, although the girdle is better developed than in *marina*, it embraces rather fewer segments.

The notopodia are more massive in *claparedii* than in *marina*, and so are the individual notopodial chaetae. The neuropodia are short in the more anterior segments and lengthen posteriorly, but they never approach the ventral line as closely as in *marina* (Fig. 8). Even in the hinder segments, the ventral ends of the neuropodia are separated by a distance about equal to the length of a neuropodium. The parapodial girdle extends from the lower end of the neuropodium to the side of the ventral groove, even in those hinder segments in which it has disappeared from the dorsal surface.

Nephridiopores are present on segments v to ix inclusive.

Arenicola ecaudata

In this species, the reduction of the ordinary annuli of the more anterior segments is least marked, the formula being:

i.3.ii.4.iii.4.iv.4.v ...

In many specimens, all of the annuli are prominently developed, and the truth of the above formula is obvious. In others, however, there is a tendency to reduce the ordinary annuli which lie immediately in front of the chaetigerous annuli, and when this occurs it affects all of the first three or four segments. The reduced annuli may in extreme cases be so small, and so overhung by the following chaetigerous annuli, as to be invisible on surface inspection. The formula then appears to be:

i.2.ii.3.iii.3.iv.4.v ...

Nevertheless, in all examples examined by myself, a sagittal cut with a razor blade reveals the hidden rings, and shows that the formula is in fact as previously stated.

The parapodial girdles of this species are rather poorly developed, as the low degree of reduction of the annuli perhaps suggests. The hinge lines lie near the front margins of chaetigerous annuli i–iii, instead of bisecting them as in the other two species. The various components of the parapodial girdle are all present, but they are small, and all localized in the front part of the annulus. In a posterior direction these structures get gradually less and less well defined, until they can no longer be made out on the dorsal surface, as from about segment xiv. In other words, although less well developed than in the other species, they concern about twice as many segments. Now the most anterior gill, in *ecaudata*, is typically on segment xvi; as in *marina*, this gill is generally small and sometimes absent. The whole arrangement evidently confirms the idea, already suggested by the other two species, that the gills and the parapodial girdles tend to exclude each other from the dorsal surface.

The notopodia are relatively smaller, and more dorsally placed, than in the other species (Fig. 8). The neuropodia are exceedingly long, extending from the side of the nerve cord to a point well above the nephridial line. In the more anterior segments, far from being short (as in *marina* or *claparedii*), the neuropodia of *ecaudata* are best developed, and reach from the ventral line to the bases of the notopodia (Fig. 4).

Nephridiopores are present on segments v to xvii.

THE ANTERIOR REGION ('HEAD')

The 'head' is the roughly conical region extending forwards from the anterior margin of the first chaetigerous annulus (Fig. 4). Its segmentation is largely obscured, in the adult, by its profound functional modifications. It consists of the prostomium and a second large portion which, to quote Ashworth (1912),

> in most adult specimens of *Arenicola*, is divided by encircling grooves into three or four (or more) rings. There are good reasons for stating that this is composed of the peristomium and a body segment which is without chaetae in the adult. In post-larval stages of *A. marina* and *ecaudata*, the region between the prostomium and the first ordinary chaetiferous segment is subdivided by a groove into two parts. The anterior and usually rather smaller portion is undoubtedly the peristomium; it never bears chaetae, but the paired statocysts may be seen near its anterior margin. The posterior of the two parts is, in the post-larval stages which the writer has examined, achaetous, but a chaeta has been observed in this segment, in either *A. marina* or *A. ecaudata*, by Professors Ehlers, Benham, Mesnil and Fauvel, a fact which demonstrates that this is a true segment. Evidence confirmatory of this interpretation is afforded by the arrangement of the giant nerve cells. In later post-larval stages in which the annulation is making its appearance, the peristomium and the segment in question become subdivided into secondary rings.... The composition of this region is probably constant throughout the family.

Except for the important study of the statocysts by Ehlers (1892), previous writers on this region have mainly confined themselves to cursory accounts of its external features, and discussions of its segmental homology. Many interesting features, especially the musculature, have received little or no attention. The following account omits the proboscis, and certain special structures (e.g. the retractor muscle) associated therewith. I hope to describe them, with the internal anatomy in general, at a later date.

Arenicola marina

Apart from the absence of parapodia, the most noteworthy specializations of the body wall of the anterior region may be grouped under the following headings: (i) the mouth, (ii) the prostomium and nuchal pouch, (iii) the central nervous system, (iv) the metastomial muscle, and (v) the statocysts.

At the *mouth*, which is terminal, the layers of the body wall continue on to the eversible proboscis. The latter organ is partly extruded in Figs. 9 and 10.

The *prostomium* may be completely withdrawn into the *nuchal pouch*, which lies behind it. The general relations of these structures can be seen in Figs. 9–13. The pouch (*nuch.p.*, Figs. 10B, 13) opens by a crescentic slit just above the prostomium (*prost.*); its roof is thin and flexible; its floor is the prostomium itself. The latter organ, when fully exposed, has roughly the form of an

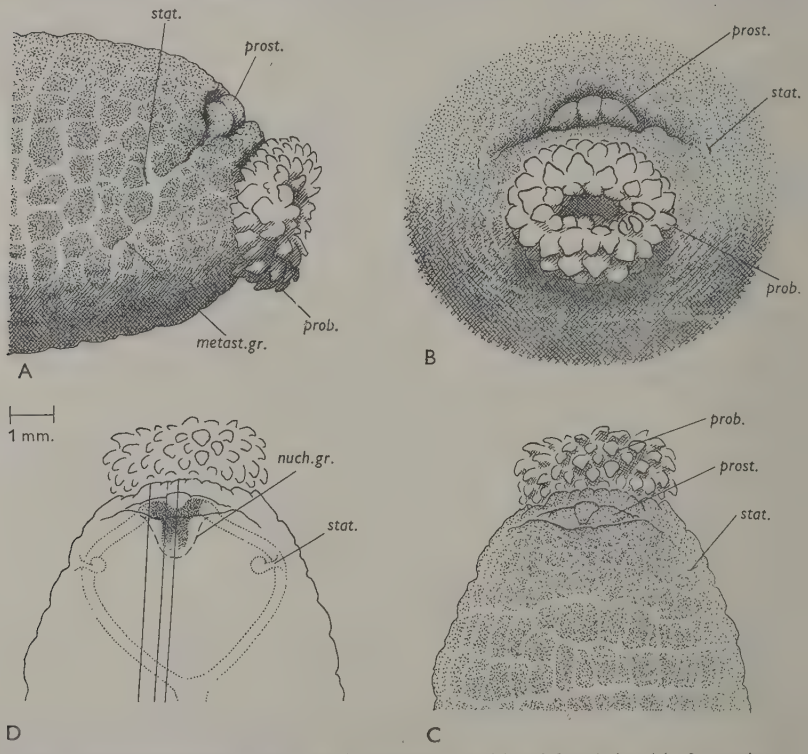

Fig. 9. *Arenicola marina*. Lateral view (A), anterior view (B) and dorsal view (C) of a specimen killed in the relaxed attitude by the Mg-formalin method. D, outline of the dorsal view, with the positions of the brain and oesophageal connectives included; that part of the brain which adheres to the dorsal surface of the prostomium is stippled; the nuchal groove is shown as a dashed line; the ruled lines give the positions of the sections in Fig. 12. Lettering as on p. 44.

isosceles triangle with its apex directed backwards; its dorsal face is impressed by a shallow Y-shaped groove (Fig. 10A). The worm must, however, be dissected if the whole prostomium is to be seen. In preserved material, it is always more or less completely overlapped by the dorsal lip of the nuchal pouch, so that one sees only its anterior margin; this is trilobed, owing to the

fact that the arms of the dorsal, Y-shaped groove continue down the anterior face of the prostomium. Between the prostomium and the mouth is a strip of body wall, which Ashworth (1912) terms the 'upper lip'.

The nuchal pouch as a whole may be regarded as a blind in-pushing of the epidermis and subjacent connective tissue, passing through the circular and longitudinal muscle layers. In sections, a large amount of transversely running muscle can be seen immediately ventral to the prostomium. Its position and course suggest that it is circular muscle; in fact, however, as will be shown below, it is made up of certain specialized muscles, derived, largely at least, from the longitudinal layer (the metastomial muscle, and the dorsal muscle of

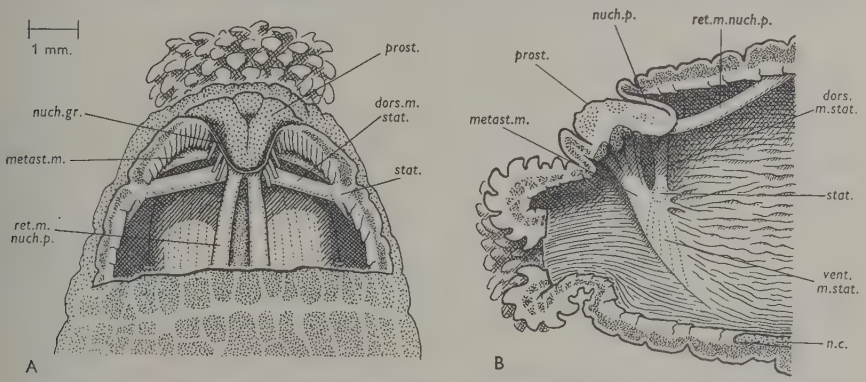

Fig. 10. *Arenicola marina*. A, dorsal dissection of the animal of Fig. 9; part of the body wall and the thin roof of the nuchal pouch have been removed. The front part of the dorsal vessel (stippled) can be seen between the retractors of the nuchal pouch. B, lateral dissection of another worm to show the coelomic aspect of the body-wall muscles of the right side; the animal has been bisected in the median plane and the gut and blood vessels have been removed. The ventral muscle of the statocyst is seen as a series of fine strands (dotted lines) running ventrally across the face of the metastomial muscle. Lettering as on p. 44.

the statocyst). The columns of the longitudinal layer pass by the sides of the nuchal pouch, and those immediately adjacent to it send slips which are inserted on its walls and help in its retraction. The chief part in retraction, however, is played by a paired muscle, the retractor of the nuchal pouch, clearly derived from the longitudinal layer, and running from the hind end of the pouch to a point on the body wall, about half way between the prostomium and the first chaetigerous annulus (Figs. 10 and 13, *ret.m.nuch.p.*).

My impression is that retraction of the nuchal pouch never occurs as an isolated act, but only when the anterior end as a whole is shortened and thickened, as part of the general movement. There are no protractor muscles. Extrusion of the proboscis is presumably due to the pressure of the body fluid, and occurs, I believe, whenever the head as a whole lengthens and narrows, and at no other time. Fig. 11, drawn from preserved specimens, illustrates

two configurations within the range that can be seen in the living animal. When the living worm assumes the extended attitude, the roof of the nuchal pouch evaginates and can be seen as a crimson transverse ridge, just behind the prostomium.

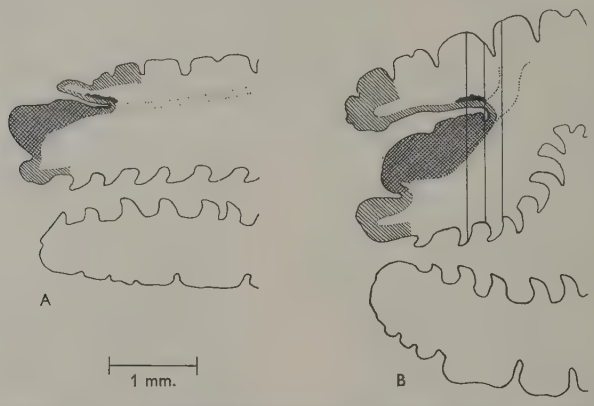

Fig. 11. *Arenicola marina.* Median sagittal sections of specimens killed as follows: A, in Mg-formalin; B, in Bouin without previous narcosis. The ruled lines in B give the planes of the sections in Fig. 13. Part of the body wall is shaded to show its thickness, and the prostomium is cross-hatched. The position of the retractor muscle of the prostomium is given as a dotted outline. The proboscis is fully withdrawn in both specimens.

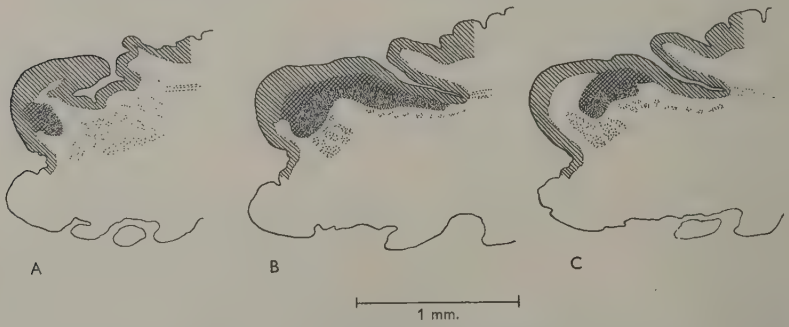

Fig. 12. *Arenicola marina.* Sagittal sections of a Mg-formalin specimen, corresponding approximately to the ruled lines in Fig. 9D. The proboscis is fully withdrawn. The superficial (ganglionic) part of the brain is cross-hatched, and the deep (fibrous) part is closely stippled. Section C is median.

The hinder part of the roof of the nuchal pouch bears a curious vascular plexus, shown black in Fig. 11. This marks what is evidently an important structural differentiation of the roof. In the region of the plexus, the roof consists of a very deep columnar epithelium without a subjacent muscular

layer. Elsewhere, it has a shallower epithelium and a thin circular muscle layer, continuous with the circular muscle layer of the general body wall. Now in the other two species, as we shall see, the prostomium cannot be retracted, and its hinder margin is marked by a nuchal groove, whose epithelium is very deep, ciliated and presumably sensory. This evidently corresponds to the hinder, vascular part of the roof in *marina*. The non-vascular part, present only in *marina*, is simply attenuated body wall, and it is this which converts the whole region into a pouch and makes retraction of the prostomium possible.

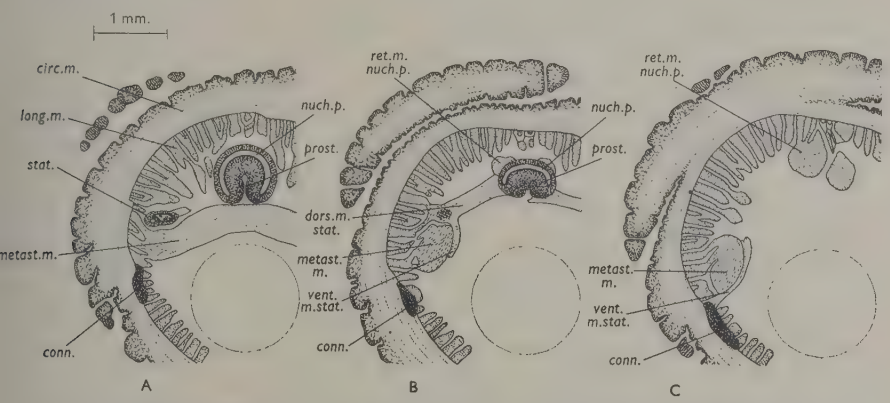

Fig. 13. *Arenicola marina*. Three transverse sections, corresponding approximately to the ruled lines in Fig. 11B, of a specimen killed in Bouin. The sections are equidistant and 0·2 mm. apart; the most anterior is on the left. The dotted circle gives the position of the gut. Lettering as on p. 44.

The general plan of the *central nervous system* of the head is shown in Fig. 9D. The ventral nerve cord continues forwards for a short distance on to the head; it then divides to give rise to the connectives, which run obliquely upwards and forwards to the prostomium. Just as the course of the ventral cord is marked externally by the ventral groove, so that of the connectives is marked by the more or less evident metastomial grooves (Fig. 9A, *metast.gr.*). The connectives resemble the ventral cord in consisting of a superficial ganglionic and a deep fibrous part, and in lying deep to the circular muscle layer (Fig. 13, *conn.*). When they reach the lateral corners of the prostomium, where the nuchal pouch pushes through the circular layer, the ganglionic part of the connectives enters into intimate relation with the epidermis. The nerves now expand somewhat and, remaining in close contact with the epidermis, pass up the front face of the prostomium to reach its dorsal side. Here they run backwards for a short distance to meet each other in the median plane. From their point of union, a pair of massive nerves runs back to the nuchal groove. That part of the central nervous system which lies in the prostomium,

in intimate relation with the epidermis, is generally termed the brain. Its form can be seen in Figs. 9D and 12. For the fine structure of the brain, see Gamble & Ashworth (1900).

The shallow grooves, which divide the anterior margin of the prostomium into three lobes and trace a Y on its dorsal face, give the line along which the brain adheres to the epidermis. The body wall is therefore thick under these grooves. At the sides of the prostomium, and in its median anterior lobe, the body wall is thin and the coelome comes near the surface (Fig. 12).

Immediately dorsal to the connectives, over the more ventral part of their course, lies the largest special muscle in the body wall of the worm. This—the *metastomial muscle*—originates as a union of contributions from all the

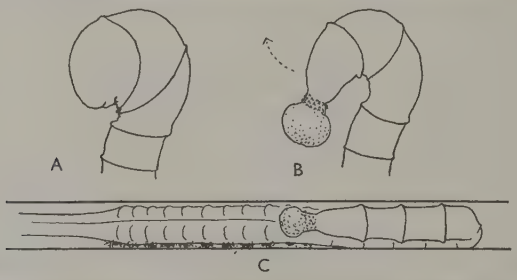

Fig. 14. *Arenicola marina*. Sketches to illustrate the process of reversing in the tube (see text).

longitudinal muscle columns ventral to the notopodial line. It runs forwards and upwards, following the general course of the connectives, until it reaches the level of the statocysts; it then leaves the inner face of the longitudinal layer and crosses the body cavity, just below the brain, to continue into its fellow of the opposite side (Figs. 10, 13, *metast.m.*).

This muscle was first described by Ehlers (1892), who said that it was inserted on to the prostomium. It is briefly mentioned by Gamble & Ashworth (1898) and by Ashworth (1904), who regard it as a retractor of the prostomium. Its true anatomical relationships, however, show that it cannot play that role. Its actual function is quite different, and very important. The lugworm sometimes reverses itself, either in its own burrow or in glass observation tubes, by narrowing its body and then burrowing (with continual extrusions of the proboscis, and uprisings of the parapodial girdles) along its own ventral surface. In this way it can turn in a tube which, at other times, it seems comfortably to fill (Fig. 14C). The problem now arises, how does this performance start? Living worms, when watched,[1] can occasionally be seen to assume a remarkable

[1] To study the movements of the proboscis and head, it is convenient to tie the whole worm with fine string about at the level of chaetigerous annulus v, to cut away everything behind the ligature, and to put the isolated front end in sea water under a binocular microscope. The preparations stay active for hours, and frequently show the turning attitude described above.

attitude, in which the dorsal wall of the head and of the first two or three segments is greatly distended, while the ventral wall shows extreme longitudinal contraction (Fig. 14A). The prostomium and mouth are thereby come to be directed backwards: the attitude can be roughly imitated by 'burying one's chin in one's chest'. Now the assumption of this attitude always heralds an outburst of proboscis activity. The first extrusion begins while the worm is still in the attitude, and the proboscis therefore emerges in a tailward direction. As this extrusion completes itself, the whole anterior end assumes a more usual configuration. If the worm is lying in a dish of sea water, this results in a forward swing of the proboscis (Fig. 14B); but if the worm is in a tube, the forward swing cannot occur, and subsequent extrusions, made in the usual manner, will serve to pull the head farther and farther along the worm's ventral surface (Fig. 14C). The metastomial muscle runs like a sling over the mouth, and, if it contracts simultaneously with the more ventral longitudinal columns from which it arises, will play an important and perhaps essential role in the assumption of the attitude of Fig. 14A.

The *statocysts*,[1] whose form was beautifully described by Ehlers (1892), are a pair of blind in-pushings of the epidermal layer of the body wall, which pass through the circular muscle layer (Figs. 9, 10, 13, *stat.*). Their openings are slit-like and dorsi-ventrally elongated. Each leads into a tube with a lumen of the same form, and which opens forwards at its deep end into a spherical bulb. The whole organ is therefore rather retort-shaped. It contains various foreign objects, such as quartz grains, fragments of spicules and diatom shells, etc., covered with more or less well-marked layers of a 'chitinoid' secretion (Ashworth, 1904).

The statocyst is provided with a rather complicated musculature, whose functions are obscure. The muscles are: (i) the dorsal muscle of the statocyst (Fig. 10B, *dors.m.stat.*), which runs dorsally and medially; its more anterior fibres continue into the corresponding muscle of the opposite side, while its hinder ones are inserted into the posterior end of the nuchal pouch, just below its retractor; (ii) a number of slips of muscle running back to the longitudinal columns adjacent to the statocyst; (iii) the ventral muscle of the statocyst (Figs. 10, 13, *vent.m.stat.*), which crosses the metastomial muscle, as a thin sheet or as a series of fine strands, to the tissue round the connectives. On the whole, it seems likely that the dorsal muscle of the statocyst is derived, as the metastomial muscle is, from the longitudinal layer; the anatomical relations of the ventral muscle, on the other hand, are consistent with its being a member of the oblique muscle series.

[1] The statocysts lie at the level of the notopodia; as they are invaginations producing a chitinoid secretion, and as the notopodial chaetae have sensory nerve endings round their bases (Retzius, quoted by Ehlers, 1892), it is tempting to think of them as the peristomial notopodia. The idea was discussed at length by Ehlers (1892), who decided against it, on the ground that certain polychaetes of other families have statocysts, neuropodia and notopodia in the same segment.

According to von Buddenbrock (1912, 1913), the statocysts of *Arenicola* are used to guide the worm when burrowing down into the mud.

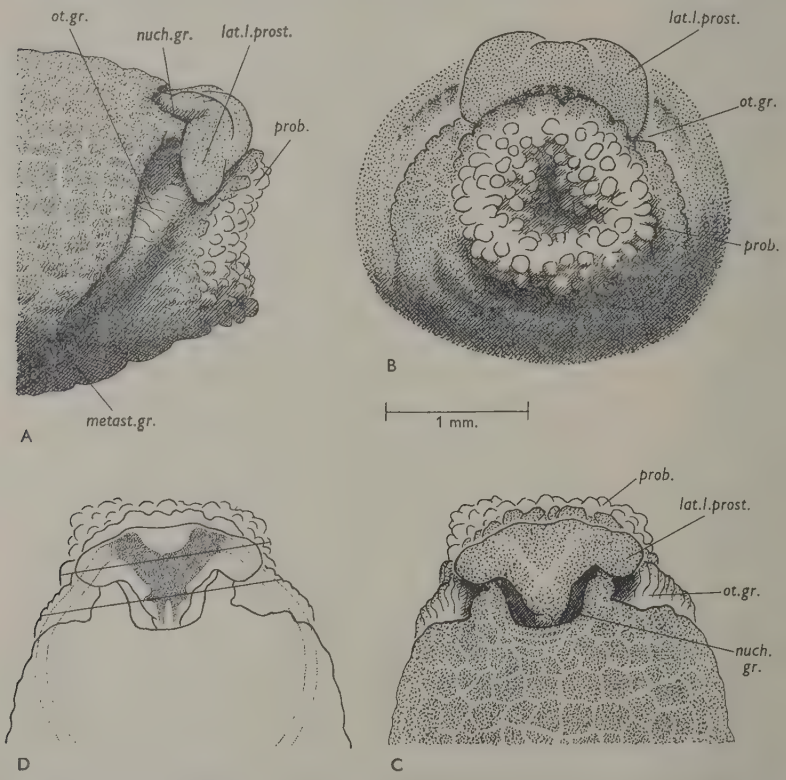

Fig. 15. *Arenicola claparedii*. Lateral view (A), anterior view (B) and dorsal view (C) of a Naples specimen killed by the Mg-formalin method. D, outline of the dorsal view with the brain and connectives given as in Fig. 9D; the ruled lines give the positions of the transverse sections in Fig. 17. Lettering as on p. 44.

Arenicola claparedii

The prostomium of *claparedii* differs in two important respects from that of *marina*. In the first place, it is prolonged laterally into two large, vertical flaps, the lateral lobes (Fig. 15, *lat.l.prost.*). In the second place, it is not retractile; nuchal pouch and retractor muscle are lacking (Fig. 16D). The nuchal groove lies, as in *marina*, round the sides and hind-end of the prostomium (Figs. 15, 17, *nuch.gr.*). It will be seen, on comparing Figs. 9 and 15, that the prostomium is relatively larger in the latter. This results, partly at

Fig. 16. *Arenicola claparedii*. American specimens, killed by means unknown to the writer. A, B, dorsal and lateral views of the same specimen. C, sagittal section of the same, cut along the ruled line in A, to show how the lateral wing of the prostomium (cross-hatched) overhangs the otic groove. D, median sagittal section of another specimen, for comparison with Fig. 11.

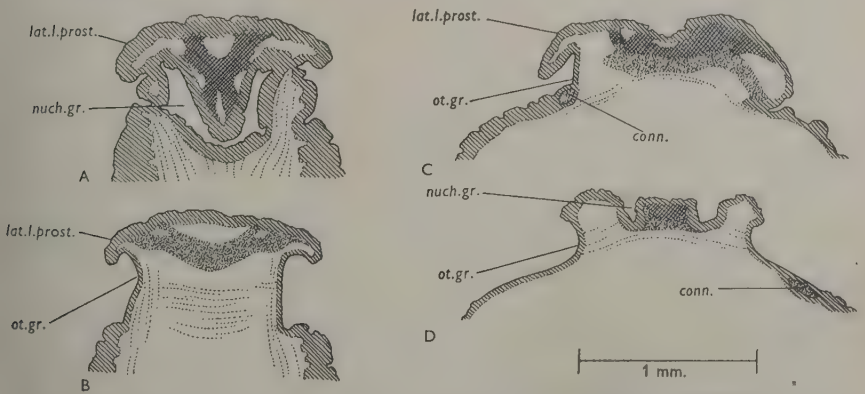

Fig. 17. *Arenicola claparedii*. Naples specimens, killed in Mg-formalin. A, horizontal section through the nuchal groove and the superficial part of the brain. B, horizontal section through the otic grooves and the deep part of the brain. C, D, transverse sections, corresponding approximately to the ruled lines in Fig. 15D. Conventions as in Fig. 12. Lettering as on p. 44.

least, from the difference in size of the two worms. Fig. 15 was drawn from a small, Neapolitan *claparedii*. In Fig. 16, which is from a Pacific specimen of comparable size to the *marina* of Fig. 9, the prostomium (after subtracting the lateral flaps) is of about the same relative size.

The central nervous system in the head of *claparedii* is very similar to that of *marina*, except that the connectives of *claparedii*, like its nerve cord, lie outside the circular muscle and in close relation to the epidermis. The connectives run up the front face of the prostomium, medial to the lateral lobes (Fig. 15D).

There is a powerful metastomial muscle in *claparedii*, having the same relations as in *marina*.

The most striking differences between the heads of the two species are the absence of statocysts, and the presence of a new structure, which will be termed the *otic groove*, in *claparedii*. Both points were noted by Ehlers (1892), who regarded the otic groove as homologous with the statocyst; but as he worked with preserved, very contracted material, his account of the groove is not wholly correct.

In the Neapolitan specimen of Fig. 15, preserved in the relaxed attitude by the Mg-formalin method, the otic groove is seen as a large, open shelf, slightly overhung behind by the body wall. It begins at a point just above the metastomial groove, and nearer the ventral surface of the worm than the dorsal, and it runs upwards and forwards towards the prostomium.[1] It ends, lateral and rather ventral to the nuchal groove, in a vertical wall (Figs. 15A, 17). Strands of muscle run across, below the brain, from the otic groove of one side to that of the other; these are indicated in Fig. 17D; if the otic groove indeed represents the statocyst, they might be its dorsal muscle.

The otic grooves, so obvious in relaxed animals, may be very difficult to detect in contracted ones. The reason is that they are closed, partly by the pressing together of their dorsal and ventral borders, and partly by means of the lateral lobes of the prostomium (Fig. 16C). The groove appears to play an important part in the life of the worm, since its surface is thus protected, even though the prostomium is left exposed, and one naturally thinks of a sensory function to compensate for the lack of statocysts. However, as pointed out by Ehlers (1892), the groove is lined by an unusually low cylindrical epithelium, rather like that of the interannular grooves; it is neither conspicuously glandular, nor nervous, nor ciliated; in a word, 'ein sehr indifferentes'.

[1] The otic groove was described by Gamble & Ashworth (1900, p. 501) as 'an enlargement of the metastomial groove' and they deny the suggestion of Ehlers that it represents the statocyst. The two grooves, however, are distinct and easy to distinguish at the ventral end of the otic groove, where they run rather parallel and with the otic groove slightly dorsal to the metastomial.

Arenicola ecaudata

The general appearance of the head in *ecaudata* is different in many ways from that of *marina*. The nuchal groove is very long, resembling in shape a U whose vertical limbs have been bent outwards, their tips reaching more than half way towards the ventral line. The area between this groove and the mouth is divided more or less obviously by a transverse fold, which separates the upper lip in front from the prostomium behind. The latter is a flat area,

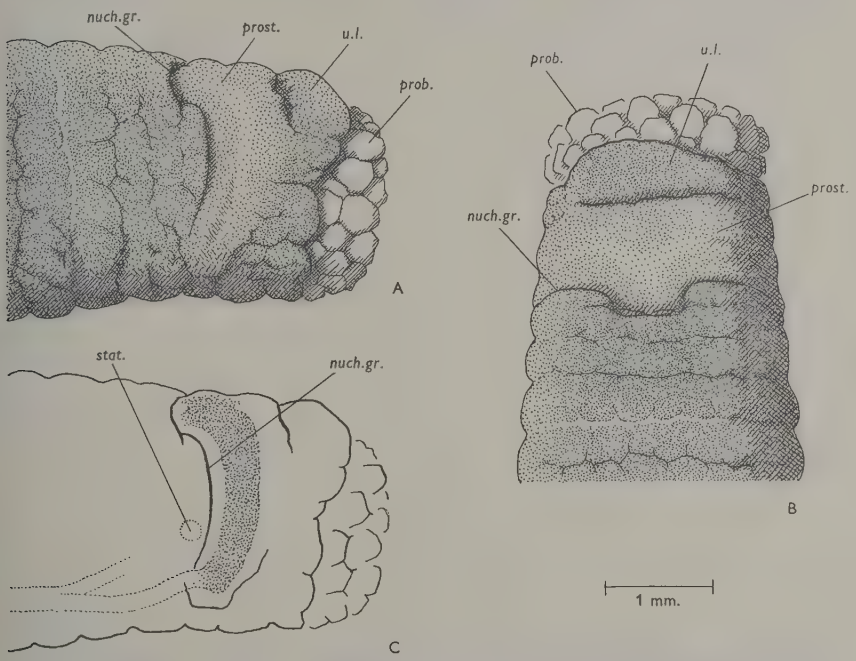

Fig. 18. *Arenicola ecaudata*. Lateral view (A) and dorsal view (B) of a specimen killed in Mg-formalin. C, outline of the lateral view, with the positions of the right statocyst and the central nervous system indicated; the part in relation with the epidermis is stippled. Lettering as on p. 44.

often hardly distinguishable from the general body wall; but in good specimens, a broad, rather smooth, very shallow depression, corresponding to the Y-groove on the prostomium of *mårina* and indicating the position of the brain, can be seen; this depression is drawn pale in Fig. 18. The prostomium extends slightly farther ventrally than does the nuchal groove. There is no nuchal pouch, and the prostomium is obviously not retractile (Fig. 19).

The connectives resemble the nerve cord in lying deep to the circular muscle layer, from which they are separated by a coelomic space. On reaching the corners of the prostomium, they enter into close relation with the epidermis,

and proceed dorsalwards as the brain. This organ is dotted in Fig. 18C; its outlines are, however, rather ill-defined and it gives off numerous nerves to the nuchal groove and the anterior body wall.

The form of these structures in *ecaudata* can be derived from that in *marina* by supposing that the corners of the brain and prostomium are dragged for a great distance in a latero-ventral direction. It will be noted that the brain is relatively large. 'Le cerveau est relativement developpé pour une Arénicole' wrote Fauvel (1899*a*), and in this respect he was more exact than Gamble & Ashworth (1900), who wrote of 'the suppression of the prostomium' and of 'the reduction of the prostomium, and, *pari passu*, the simplification of the brain'.

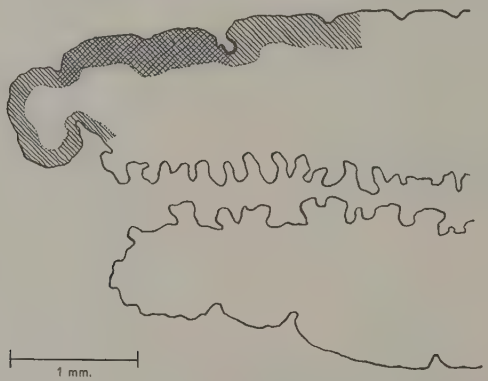

Fig. 19. Median sagittal section through the head of *Arenicola ecaudata*. Compare Figs. 11, 16D.

The statocyst is a spherical sac with no duct to the exterior; it contains 'spherical, oval and lenticular chitinoid bodies...there is at first only one statolith. Later many others are formed, but the original one remains conspicuous by reason of its larger size' (Ashworth, 1912). It corresponds in position with the statocyst of *marina*, and lies on the superficial face of, and partly embedded in, the longitudinal muscle layer. It receives a nerve from the connective, shortly before the latter enters the brain.

Owing to the smooth face which the longitudinal layer presents to the coelome in this species, the special muscles of the head are hard to make out in dissections. However, examination of the cleared and flattened body wall with polarized light shows that a metastomial muscle exists, having essentially the same relations as in *marina* or *claparedii*.

THE POSTERIOR REGION ('TAIL')

For many decades, the genus *Arenicola* has been divided into 'caudate' and 'ecaudate' sections. All the species have a head, whose characters have already been noted. This is followed, in the 'caudate' species, by a number of trunk segments with parapodia, and in which all the septa, except the first, third and fourth, have practically disappeared; and this again by the tail, in which appendages are lacking but the septa persist. The number of trunk segments varies, in different 'caudate' species, from 16 to 20. The 'ecaudate' division consists of two species, *ecaudata* and *grubii*. In *ecaudata*, the head is followed by a trunk region resembling in many points that of the 'caudate' species; for example, it lacks septa except for i, iii and iv; the vessels of septum vii are specialized to form the hearts; and so on. The first gill, however, is rather farther back; on chaetigerous annulus xv instead of vii. There follows a rather gradual transition (through segments xvii to xix) to a region in which the septa persist, and which is externally distinguishable from the trunk.[1] In the trunk segments, the four annuli that separate any two chaetigerous annuli are very equal in size and pigmentation; in the tail, on the other hand, the second (and sometimes the third) of the four is rather larger and more deeply coloured than the others; this gives the tail as a whole a banded appearance, except in the darkest specimens. It seems clear enough that a differentiation exists, corresponding to, though less profound than, that of the 'caudate' species. A similar differentiation, a couple of segments farther forwards, is traceable in *grubii*. However, it is with *marina* and *claparedii*, in which the tail is most distinctively specialized, that we shall now be concerned.

Arenicola marina

The fact that the tail segments of *marina* are short at its base and lengthen towards the tip, is suggested by surface inspection and established by dividing the tail horizontally (Fig. 20). The fact is interpreted by Ashworth (1912) as follows: 'During development, new chaetiferous segments are formed immediately in front of the terminal segment or pygidium. In the ecaudate species all the segments are produced in this growing zone, the activity of which becomes exhausted at about the end of the post-larval stage. In the caudate species, after the full number of chaetiferous segments has been formed, new segments are evidently produced at the anterior end of the tail; for in this region each segment is short from before backwards, while in the middle and posterior regions of the tail the segments are longer, and, in adult or late post-larval specimens, are subdivided into annuli.... In *A. marina* there may be 60 to 70 tail segments, though usually there are fewer owing to losses posteriorly.'

Now horizontal sections, either of large or small *marina*, never show a new segment in the act of formation at the base of the tail. The animal of Fig. 20 is

[1] This distinction is clearer in preserved than in living worms.

typical; even the shortest tail segments have a definite and uniform length (in this case, of 3 annuli), and the foremost of all is rather longer than those which follow it. Having examined many specimens, I do not believe that there is any formation of new segments at the tail base.

Fig. 21 gives the number of annuli per segment in three worms of different size, and affords a representative picture of the mode of growth of the tail. The counting of the annuli was not always exact, because it is sometimes doubtful whether an incipient annulus, in process of formation, should be counted or not: the use of smoothed curves is therefore legitimate. As the worms grow, the segments evidently lengthen; segment xv, for instance, has 2, 6 and 12 annuli in the three worms; and this growth becomes more rapid tailwards.

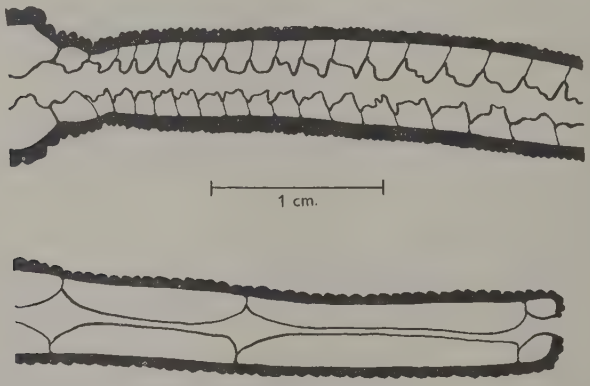

Fig. 20. Horizontal sections through the base and tip of the tail of an *Arenicola marina* of overall length 140 mm.

The following interpretation is suggested. The pygidial growth zone first lays down the trunk segments, then a great number of tail segments; these are at first very short and serve as a reserve stock; then they lengthen, the hinder ones more rapidly than the front. The graph clearly shows that losses from the hind-end must occur, not only as accidents but of necessity, as the hinder segments would otherwise become impossibly long. The worms in the graph had 44, 28 and 18 tail segments, in ascending order of size.

The reason for this fountain of tail production is not obvious at first sight. The hinder segments may be nearly 2 cm. in length; if the largest worm of Fig. 21 started with the '60 to 70 tail segments' which Ashworth gives as the maximum for this species, it has clearly lost about a metre of tail or potential tail; more than five times its overall length at death. The method adopted by *ecaudata*, of growing a tail of appropriate length and tolerating such losses as may occur, would seem more economical. 'Adult specimens of this species',

wrote Ashworth (1912) of *ecaudata*, 'seldom exhibit as many segments as they possessed at the end of the post-larval stage, but occasionally an unabbreviated example is met with, in which case the number of segments is about 60 to 64.

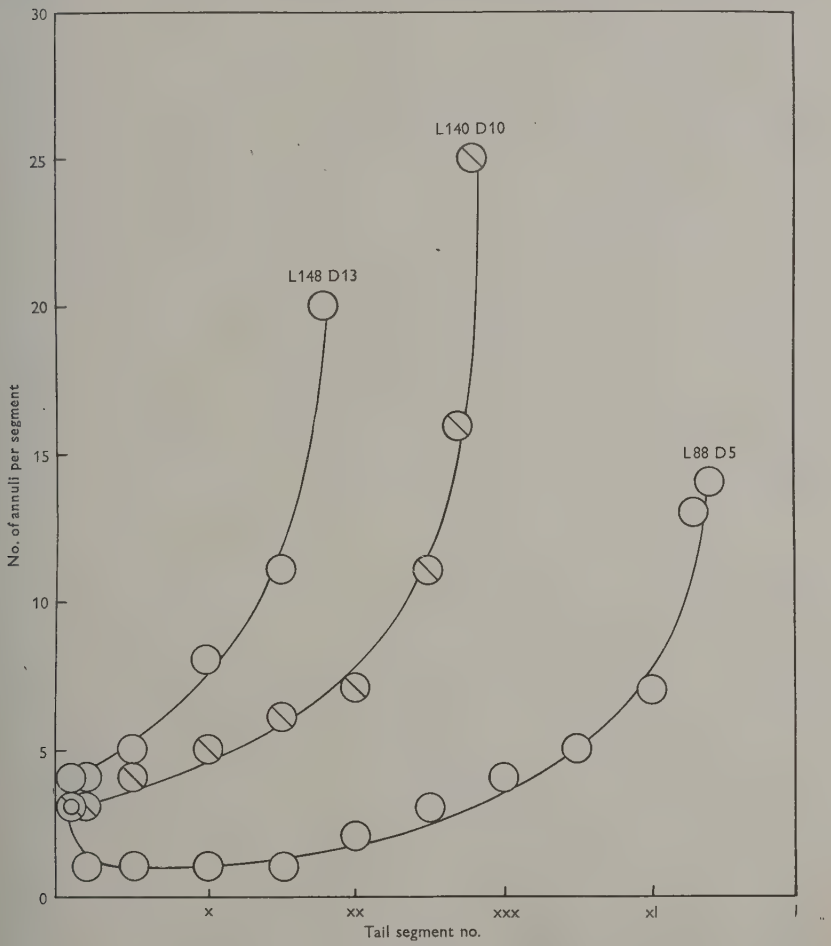

Fig. 21. The number of annuli per tail segment in three specimens of *Arenicola marina*. The total length, and trunk diameter, are given, in mm., by the graph of each specimen.

There are about 45 to 50 segments in average specimens.' These figures include trunk segments. An average *ecaudata*, then, starts with 60-odd segments, of which it loses 20 or 25%; a large *marina* has lost more than 50% of

its initial 80 or 90; and the lengthening of the segments in *marina* makes its losses the greater in proportion.

As already noted, *marina* generally lives on muddy sand flats, while *ecaudata* is found in sandy material among stones or the breakdown fragments of rocks. The sand-flat habitat involves a high degree of exposure of the tail. Lugworms make periodic backward excursions to the surface to defaecate, at which moments their tails are vulnerable to those predators which do not resent a high proportion of roughage in their diet. At low tide, sea birds may intervene. Stach (1944) writes of *A. loveni*, a Southern species very similar to *marina*, that 'The oyster catcher (*Haematopus fuliginosus*) was often observed to peck off the tails of lugworms extruding their castings'. High tide will doubtless bring other predators. Evidently, a tail which contains no very essential organs, which shortens rapidly at a touch, and which grows from reserve segments at the base, is appropriate. Moreover, the tail is also exposed to physico-chemical assault. The falling tide often leaves pools or shallow sheets of water over the burrows of *marina*, and these may become hot enough in bright sunshine, or dilute enough after a violent rainfall, to be injurious to the worms. Their behaviour under such conditions was discussed elsewhere (Wells, 1949*a*). They appear to make backward 'testing excursions' from time to time towards the surface, and only when the returning tide has brought cooler or more saline water do they pump it through the burrow to get the oxygen they need. Once again, it is the tail which bears the brunt of the injurious conditions, and its renewal is the more intelligible.[1]

Arenicola claparedii

It was already noted by Ashworth (1912) that Neapolitan specimens of this species are on the whole much smaller than Pacific ones. In both, the tail appears to consist of few segments, with a much less well-marked size gradient than in *marina*. My Neapolitan specimens are mostly 40–60 mm. in length, of which about a quarter is tail; there may be 12 tail segments, but usually the number is 5 or 6, and the last segment is seldom much more than twice as long as the first. Thus, a typical specimen measures overall 41 mm.; this includes a tail with 5 segments, of lengths 1·7, 2, 2·3, 3 and 3·6 mm. My Pacific specimens have only 2 or 3 tail segments, all of about equal length; they are, however, badly preserved and may have autotomized some tail segments in the process. The three Pacific specimens at the British Museum all appear (from external examination) to have few—from 5 to 7—tail segments.

All of these specimens are adult, and it is difficult to discuss the significance of their tail numbers without information about the post-larval stages, which

[1] The tail is also specialized with regard to its movements. The irrigation waves, by which water is driven through the tube, typically start at the junction of trunk and tail in *marina* and move forwards. If reversed (tailward) irrigation is in progress, they die out at the junction. In *ecaudata*, on the other hand, they run forwards from the hindmost end of the body. It appears likely that the tail of *marina* is responsible for the very rapid ejection of the faecal cylinders.

does not appear to be available. Similar tails occur in *A. cristata* Stimpson, at Wood's Hole, and for this species the development is known. Ashworth (1912) writes of adult American *cristata*, that the tail usually consists of 7–10 segments. By the kindness of Prof. Ritchie, of the University of Edinburgh, I have been allowed to dissect one of Ashworth's largest specimens; its overall length is 434 mm., and it has 7 tail segments, measuring, from base to tip, 12, 16, 17, 18, 19, 23 and 31 mm. Now the development of *cristata* was described by Lillie (1905), and the post-larva is figured by Ashworth (1912). The pygidial growth zone forms about 40 tail segments before its activity ceases, and, in the post-larva, these show a beautiful size gradient, as in adult *marina*. Apparently *cristata* resembles *marina* in the essential mechanism, but its reserve is smaller, and is often more completely spent. The same may be true of *claparedii*.

Summary

Worms for dissection, or for museum preservation, should be prepared by the magnesium-formalin method, of which two modifications are given in the text.

The body of *Arenicola* is differentiated into: (*a*) an achaetous 'head', comprising the prostomium and a small number (probably two) of subsequent segments, (*b*) a 'trunk', composed of a number, varying somewhat with the species, of chaetigerous segments, and (*c*) a '*tail*', which may or may not be chaetigerous according to the species. The method of subdividing the body according to the distribution of the gills, so often met with in the literature, is misleading because it conceals the very fundamental differentiation between 'head' and 'trunk'.

The main layers of the body wall are described. There are grounds for supposing that the circular muscle layer plays a greater part than the longitudinal in the maintenance of a postural fluid pressure in active worms.

The parapodial derivatives are the neuropodia, the notopodia, and the parapodial girdles; details of all three, and especially of their musculatures and movements, are given in the text. The extent to which these structures are developed varies from species to species, as well as from segment to segment within a species; the latter differentiation (at least in *marina*) corresponds to functional differences in the attitudes and movements of the segments. *Claparedii* differs from *marina*, chiefly in the great development of the parapodial girdles of the more anterior trunk segments, with concomitant reduction of the intervening ordinary annuli, and in the comparative shortness of the hinder neuropodia. *Ecaudata* is especially distinguished by the slight development of the parapodial girdles and the length of the neuropodia, especially in the more anterior segments.

The head is the roughly conical region extending forwards from the anterior margin of the first chaetigerous annulus. All species have a metastomial

muscle, derived from the longitudinal layer, and playing an important part in the process of turning in the tube. The chief special sense organ appears to be the nuchal groove. The main differences between the three species are as follows: *marina* has a nuchal pouch into which the prostomium can be retracted; *claparedii* lacks statocysts and has, instead, a large and rather complex otic groove of unknown function; *ecaudata* has a nuchal groove and brain which extend for a great distance towards the ventral line.

The tail of *ecaudata* bears parapodia and gills; it differs from the trunk in having well-developed septa and in respect of the external annulation. The tail of *marina* is achaetous and grows backwards from reserve segments, laid down early in life, at its base. The rate of tail production in this species is great, and probably related to the hazards which the sand-flat habitat involves for the tail. The tail in adult *claparedii* has few segments. It is compared in the text with that of *A. cristata* Stimpson; and the conclusion is drawn that in both species the facts are essentially as in *marina*, but the reserve is smaller and soon exhausted.

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Appendix

Reference letters used in the text-figures

circ.m.	circular muscle
conn.	connective nerve
dest.	destruction zone
dors.l.	dorsal line
dors.m.stat.	dorsal muscle of the statocyst
dors.v.	dorsal vessel
ep. & c.t.	epithelium and connective tissue
form.	formative zone
g.	gill
h.l.	hinge line
interann.n.	interannular nerve
lat.l.prost.	lateral lobe of the prostomium
lat.neur.v.	lateral neural vessel
long.m.	longitudinal muscle
metast.gr.	metastomial groove
metast.m.	metastomial muscle
m.h.	muscles of the hinge
m.parap.c.	muscles of the parapodial canal
n.c.	nerve cord
neph.	nephridium
neph.l.	nephridial line
neph.long.v.	nephridial longitudinal vessel
neph.p.	nephridiopore
neurop.	neuropodium
notop.	notopodium
notop.b.	notopodial base
notop.l.	notopodial line
notop.long.v.	notopodial longitudinal vessel
notop.t.	notopodial tip
nuch.gr.	nuchal groove
nuch.p.	nuchal pouch
obl.m.	oblique muscle
obl.m.notop.	oblique muscle of the notopodium
ot.gr.	otic groove
parap.c.	parapodial canal
prob.	proboscis
prost.	prostomium
prot.m.neurop.	protractor muscle of the neuropodium
prot.m.notop.	protractor muscle of the notopodium
ret.m.neurop.	retractor muscle of the neuropodium
ret.m.notop.	retractor muscle of the notopodium
ret.m.nuch.p.	retractor muscle of the nuchal pouch
stat.	statocyst
stom.	stomach
u.l.	upper lip
vent.m.stat.	ventral muscle of the statocyst
vent.v.	ventral vessel

THE SEASONAL VARIATION IN WEIGHT AND CHEMICAL COMPOSITION OF THE COMMON BRITISH LAMINARIACEAE

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(Text-figs. 1–20)

CONTENTS

	PAGE
Introduction	45
Investigations on separate constituents	47
Preparation and analysis of samples	49
Results	50
Discussion	50
General	50
Laminaria cloustoni	52
Laminaria digitata	56
Laminaria saccharina	60
Preliminary examination of the haptera of the Laminarias	64
Summary	68
References	69

Introduction

In previous publications the author (Black, 1948) has reported the seasonal variation in the total ash, iodine, crude protein, mannitol, laminarin and alginic acid contents of the Laminariaceae, *Laminaria cloustoni*, *L. digitata* and *L. saccharina*, for the 2-year period from November 1944 to October 1946.

The work has been continued for a further 2 years and this paper summarizes the seasonal variation in the above constituents, with the exception of iodine, for the period November 1946 to October 1948 inclusive. In addition, the seasonal variation in the fresh weight and dry weight contents has also been recorded.

The algae, in general, undergo such marked variations in chemical composition depending on the season of the year, the habitat, and the depth at which they grow, that any analysis of a sample for which the complete history is not given is of little value.

Cast weed, which usually has all the water-soluble constituents leached out either by the buffeting action of the waves before it is finally deposited on the beach, or by rain while exposed on the shore, may also have undergone appreciable bacterial decomposition, giving a false picture of the composition of the living plant. It is quite possible, too, that the time which elapses between the collection and drying may influence the composition, so that this time, together with the conditions of drying, should also be recorded.

The present investigation has shown that the method of sampling adopted is relatively sound, and that at any one time surprisingly small differences occur in the composition of individual plants taken from the same habitat, at the same depth, and dried under identical conditions.

The investigation is unique in that the method of sampling prevented the weed from coming into contact with rain, etc., which would affect its composition, and the plants were immediately dried under controlled conditions to reduce any chemical and biological changes to a minimum. Previous workers, on the other hand, do not state how their samples were collected, whether the weed was cut, or whether the samples were those of drift weed, and in what manner their samples were dried.

Although Stanford (1883, 1884*a*, *b*, 1886) in the second half of the nineteenth century carried out the pioneer work and laid the foundations for an industry based on the organic constituents of seaweed, it was not until 1919 that Lapicque carried out the first systematic investigation into the seasonal variation in the chemical composition of the marine algae. During the first world war, however, the demand for potash led to an intensive investigation being carried out by Hendrick (1916), but he was chiefly concerned with the analysis of the mineral matter of the algae.

From 1927 to 1929, Colin & Ricard (1929, 1930) collected monthly samples of *L. flexicaulis* and *L. saccharina* and examined them for dry weight, ash, mannitol, laminarin, algin and cellulose. Lunde (1937), investigating the possibilities of the seaweed off the coast of Norway as a source of raw material, collected monthly samples of *L. digitata* from 1935 to 1937 and analysed them for ash, mannitol, alginic acid, laminarin, fucoidin and nitrogen.

Similar investigations have been carried out in Japan by Atsuki & Tomoda (1926*a*, *b*), in Russia by Kizevetter (1938) and Vedrinskii (1938), and in Eire by Dillon (1943). Our knowledge, however, of the organic constituents of the marine algae is still incomplete. Accurate methods of analysis have been devised for the estimation of mannitol, laminarin, alginic acid and cellulose, while work is continuing on a method for the estimation of fucoidin. The fats and pigments require further investigation. Their nature and relative proportions in the algae are in many cases indeterminate.

No work appears to have been carried out on the algal proteins.

Minor constituents such as fucosterol and the neutral oils are at present being investigated, and it may well be that other valuable constituents have yet to be identified.

The work described in this paper forms part of the programme of research and development on seaweed undertaken by the Scottish Seaweed Research Association.

The author wishes to thank Miss B. Graham and Mr W. Cornhill for assistance with the analytical work and the Association for permission to publish.

Investigations on separate constituents

In a brief review it is impossible to summarize all the work which has been carried out on the known constituents of the brown algae. The inorganic and several of the organic constituents have attracted the attention of numerous investigators, but it is unfortunate that often the results are somewhat conflicting.

Total ash

The total ash consists of inorganic salts, presumably in solution in the cell sap, and the cations combined with the organic constituents such as alginic acid and fucoidin. In addition, the ash figure contains salts from the sea water retained on the surface of the plant. The plants were only allowed to drip before drying, since it was not considered advisable to wash off this surface water with distilled water which might affect the composition. Until about 1850 the ash of seaweeds, chiefly of the fucoid types, was the sole source of alkali for the soap and glass industries. This kelp industry was then threatened by the Le Blanc process, but as the use of iodine in medicine developed, a new kelp industry arose based on the ash of the laminarias; but this industry is also obsolete. Any future industry, however, based on seaweed will most likely depend on its organic constituents, which are mainly polysaccharide in character.

Trace elements

The accumulation of trace elements in marine algae, which can be explained by considering alginic acid as an ion-exchange material, has been studied by Cornec (1919), Vernadskii (1930), Jones (1922), Öy (1940), and Wilson & Fieldes (1941).

A study of the trace elements present in the Laminariaceae and Fucaceae common to Scotland is at present being carried out and the results will be published in a future communication.

Mannitol

Mannitol, a hexahydric alcohol common to all brown seaweeds, was first detected in *L. saccharina* by Stenhouse (1844). It appears to be the primary product of photosynthesis, previous workers having found only traces, or the complete absence, of free-reducing sugars. Like the mineral matter, the mannitol is probably all in solution in the cell sap, for if the living plant is put into distilled water the salts and mannitol rapidly diffuse through the cell wall into the surrounding water.

Although there is a recent patent by Berk (1940) on the extraction of mannitol from seaweed, the mannitol of commerce is obtained from manna, or is prepared synthetically by the catalytic reduction of fructose.

Laminarin

Laminarin has been the subject of investigation by various workers. It was first described by Schmiedeberg (1885), who isolated it from the Laminariaceae. It has since been studied by Krefting & Torup (1909), Kylin (1913), Gruzewska (1923), Colin & Ricard (1929), Lunde (1937), Nisizawa (1940), Le Gloahec & Herter (1940), and Barry (1938, 1939, 1941, 1942), and their work has been reviewed by Hassid (1944). Barry (*loc. cit.*) showed that laminarin consisted exclusively of glucose units, and that after methylation and hydrolysis it gave 2, 4, 6-trimethyl glucopyranose. He concluded that laminarin consisted of a chain of β-glucopyranose units bent into a spiral form.

Laminarin, therefore, differs fundamentally from starch and cellulose in that the glucose residues are combined by 1, 3-glycosidic linkages and not through carbon atoms 1 and 4.

The extent of oxidation of laminarin with periodic acid was used by Barry (1942) as an end group assay for this polysaccharide, and the results indicated a chain of sixteen glucose units. This chain length was not in agreement, however, with that obtained by the Haworth-Hirst method which indicated a chain length of about seventy-four glucose units.

The present investigation has shown that laminarin, present only in the frond, can be isolated in two forms, an almost water-insoluble form from *L. cloustoni*, which separates from cold water, and a more soluble form from *L. digitata*, which can only be obtained from aqueous solution on the addition of alcohol. The two forms are at present being studied.

It is not yet known what part laminarin plays in the metabolism of the algae.

Alginic acid

Alginic acid, found in all brown seaweeds, where it is believed to play an important part in the cell wall, was first isolated by Stanford (1883, 1884*a*, *b*, 1886) and has since been studied by the following workers: Hoagland & Lieb (1915), Nelson & Cretcher (1929), Bird & Haas (1931), Dillon & McGuinness (1931), Gomez (1933), Barry & Dillon (1935, 1936), Hirst, Jones & Jones (1939), Stewart & Lucas (1940), Speakman & Chamberlain (1944), Astbury (1945), and Wasserman (1949). It has been shown to be a polyuronide composed entirely of D-mannuronic acid.

Dillon & McGuinness (1931) believed that the alginic acid in the growing plant was combined with calcium and iron, and that desiccation destroyed the colloidal character of these compounds and rendered them insoluble. Bird & Haas (1931), on the other hand, believed that the alginic acid in the cell wall was in two forms: (*a*) a water soluble form, and (*b*) the acid in the free state. Recent adsorption experiments carried out by Wasserman (1949), however, have shown that the alginic acid occurs in the cell tissue of brown algae in the form of various metal salts, and is not present as the free acid.

Crude proteins

Except for the work of Haas and co-workers (1929, 1931, 1933, 1938), who succeeded in isolating an octapeptide of glutamic acid, no other work has been carried out on the nitrogen metabolism of the brown algae.

Cellulose

Although Kylin (1913, 1915, 1918, 1944) had shown that the cell-wall constituents of various seaweeds gave, with iodine and sulphuric acid, the characteristic blue colour of cellulose, considerable doubt existed for some time as to the occurrence of normal cellulose in marine algae. Thus Atsuki & Tomoda (1926*a*, *b*) stated that the greater part of the crude fibre of the laminarias consisted of the hemicelluloses, and that there was no evidence of the normal cellulose, while Ricard (1931), in the algae examined by him, did not obtain the characteristic reaction of cellulose, as found by Kylin. On the other hand, Naylor & Russel-Wells (1934) and Dillon & O'Tuama (1935) demonstrated the existence of normal cellulose in marine algae. Viel's (1939) survey of the literature reveals numerous contradictions, but recent work by Percival & Ross (1948*a*) has shown conclusively that the brown algae do contain cellulose which is fundamentally similar to the cellulose of the land plants.

Fats

Except for the work of Russel-Wells (1932) and Takahashi and his co-workers (1933, 1935, 1939), no other work appears to have been carried out on the fats of the Laminariaceae, and there is no information on the seasonal variation. Russel-Wells (1932) showed that a correlation existed between the fatty constituents and the depth of immersion of the algae. Takahashi *et al.* have, over a number of years, studied the fats of the indigenous algae of Japan and identified the various fatty acids.

Pigments

Although an appreciable amount of work has been carried out on the pigments of the Fucaceae, those of the Laminariaceae have received very little attention, the only recent work of a systematic nature being that of Manning & Hardin (1944).

Preparation and Analysis of Samples

Each month, the samples of *L. cloustoni* were collected on the reef off Cullipool, Luing Island, in approximately 4 m. of water (D.L.W.O.S.T.), every effort being made to take them from the same spot and at the same depth. The open sea samples of *L. saccharina* were taken at Rudh-an-Aoil, Shuna Island and the sea-loch samples at Eilean Coltair, Loch Melfort, where the plants were growing in 3–4 m. of water (L.W.). As with *L. cloustoni*, the samples were obtained by trawling a multi-pronged grapnel for 2 min., hoisting the grapnel and lifting the weed into the boat.

The open-sea samples of *L. digitata* were taken at Atlantic Bridge and the

sea-loch samples at Eilean Coltair, Loch Melfort, where the plants were growing in 1 m. of water (L.W.). The samples were taken by hand at low water, when the plants were partially exposed. With each species, twenty plants were taken, measured and weighed. Two plants were selected for dry-weight determinations, and two were chosen at random for chemical analysis. The plants, separated into stipes and fronds, were draped over racks in a heated shed and dried at a temperature of 25–35° C. for approximately 48 hr., after which they were ground in a Christy and Norris No. 8 Laboratory Mill, fitted with a $\frac{1}{64}$ in. perforated plate screen, giving a powder which practically all passed through a sieve of 90 meshes to the inch. As the analytical methods were evolved it was found that this fine state of division was essential, especially for the method of estimating alginic acid.

The methods of analysis used were those previously employed by the writer (1948).

In the preparation of the samples for analysis, changes in composition due to respiration, etc., were negligible provided drying was carried out immediately after sampling; samples dried rapidly at 80–90° C. confirmed the results obtained at the temperatures employed in this investigation. On the other hand, plants killed in boiling absolute alcohol before drying, as is the normal procedure in plant analysis, showed considerable loss of mannitol and mineral matter, but it was found possible to kill sections of the laminarias in boiling chloroform without materially affecting the chemical composition.

Results

The results, calculated on the anhydrous basis for the frond, stipe and whole plant, are given in Figs. 1–19 (pp. 53–67).

Before drying, the plants were divided into stipes and fronds which were weighed separately. From these results each constituent determined in stipe and frond was calculated for the whole plant.

Figs. 2, 8 and 12, giving the seasonal variation in the dry-matter contents of the fronds, the stipes and the whole plants, can be used to recalculate any of the results (expressed on the dry basis) on the fresh-weight basis.

In Fig. 20 (p. 68) the seasonal variation in the fresh weight of *L. saccharina* from Loch Melfort and Shuna Island is given, while the average figures for the three species are given in Table I.

Discussion

General

In general, the results agree reasonably well with those of the first 2 years investigated (Black, 1948), despite the fact that the summer of 1947 was exceptionally good with considerable sunshine, while 1948 was a very poor summer with considerable cloud and rain. Slight differences are occasionally found,

however, in the spring (March–April). At this period of the year, when a marked increase in the rate of photosynthesis occurs, the plant is actively producing a new frond, while the old frond is wearing away. The composition of the old frond (as shown in Table II) differs somewhat from that of the new frond, to which it is still attached, so that conditions such as rough weather, which influence the shedding of the old frond, will have an effect on the composition of the whole plant.

It would appear, therefore, that when the older part of the frond detaches itself it still contains mannitol and laminarin while the new growth contains no laminarin. This, no doubt, accounts for the sudden drop in laminarin in the spring. The new frond then undergoes a period of rapid growth and laminarin

Table I. Maximum, Minimum and Average Weight of Plants in Grams

		Maximum	Minimum	Average of 450 plants
L. cloustoni	Frond	936	510	681
	Stipe	1787	681	1192
L. saccharina (open sea)	Frond	1022	198	595
	Stipe	227	85	198
L. saccharina (loch)	Frond	936	198	595
	Stipe	227	85	170
L. digitata (open sea)	Frond	1901	340	965
	Stipe	426	142	255
L. digitata (loch)	Frond	823	198	426
	Stipe	227	85	142

Table II. Composition of the Old and New Frond of *Laminaria cloustoni* collected at Cullipool on 14 April 1947 (Dry Basis)

	Total ash	Mannitol	Laminarin
Old frond	38·8	4·0	2·7
New frond	36·7	8·0	Trace

is absent. In general, this polysaccharide is almost completely absent when there is rapid growth, i.e. in all the laminarias in the spring, in *L. digitata* at Atlantic Bridge for the greater part of the year, in the annual *Saccorhiza bulbosa* already reported, and in all the samples of *Macrocystis pyrifera*, *Nereocystis luetkeana* and *Lessonia flavicans* so far examined.

While the percentage of laminarin in *Laminaria cloustoni* fronds is over 30 from August to December (dry basis), in *L. saccharina* and *L. digitata* it falls rapidly in September, reaching 4·7% in *L. saccharina* (open sea), 5·9% in *L. saccharina* (loch) and 7·5% in *L. digitata* (open sea). Parke (1948, and private communication) has found that growth in *L. saccharina* and *L. digitata* continues at a greater rate during summer and autumn than in *L. cloustoni*. With *L. cloustoni* fronds there was practically no growth from July to December in the sublittoral fringe zone, which confirms the author's suggestion that laminarin is generally found when there is 'restricted growth'.

In March, therefore, we find the algae high in proteins and alginic acid with

the cell sap high in mineral matter and low in carbohydrates, which have been used up during the winter in respiration and probably in the synthesis of amino-acids. In the spring a rapid increase in the rate of photosynthesis occurs accompanied by an increase in the mannitol content and a decrease in the ash content, while rapid growth of the plant results in a decrease in the crude protein content. A decrease in alginic acid occurs as a result of this increase in mannitol. As summarized in Fig. 19, when the results are calculated on the anhydrous basis, ash, proteins and alginic acid are at a maximum and mannitol and laminarin at a minimum at the beginning of the spring, while in the autumn the reverse is true.

In the first 2 years investigated, with the exception of *L. digitata* in 1948, a break or flattening out of the mannitol graph for the fronds occurs in July–August of each year. This coincides with (*a*) a slowing up in the rate of growth, (*b*) the absence of nutrients in the waters, and (*c*) the probable period of sporogenesis in the case of *L. digitata* and *L. saccharina*, so that these factors together with light which is at its maximum intensity at this time are all contributory factors influencing the chemical composition of the algae.

Fronds *Laminaria cloustoni*

In May 1947 the dry-weight content is at a minimum of 13·3% (Fig. 2), laminarin is at a minimum of 1·0% (Fig. 1), while the total ash is at a maximum 37·6% (Fig. 1). At this period the new frond has probably taken over photosynthesis and the old frond has been cast. The new frond contains 14·2% mannitol (Fig. 3) and 11·8% crude proteins (Fig. 4), the mannitol having been at a minimum in March (6·4%) and the proteins at a maximum (15%), while the alginic acid was also at a maximum (19·3%).

As the ash falls to a minimum of 13% in September-October the dry-weight content reaches a maximum of 32% in September, the alginic acid a minimum of 8%, and the laminarin a maximum of 32·4%, the ash graph (Fig. 1) being the inverse of the laminarin graph.

In 1948, maxima and minima of the same order of magnitude occur at approximately the same periods, with the exception of mannitol which is 25% from June to August compared with a maximum of 22·9% in August 1947. In general, the laminarin, dry weight and mannitol are parallel, showing minima in the spring and maxima in the autumn, while the ash, crude proteins and alginic acid are the reverse, showing maxima in the spring and minima in the autumn.

In Fig. 6 the ash graphs for the 4 years investigated are given and show that the results are reproducible within a month, e.g. an ash content of 30% occurs in June–July in 1945, 1947 and 1948, and in July–August in 1946.

The only striking difference in the composition of the fronds during the 4 years now investigated is in the laminarin content which progressively increases each year from 29% in 1945 to 34% in 1948, while later work to be

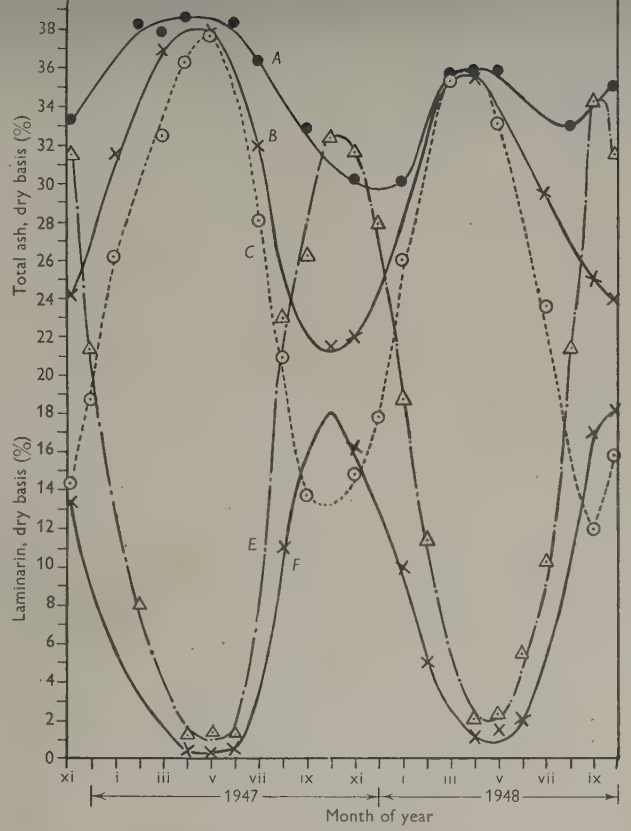

Fig. 1. Seasonal variation in total ash and laminarin in *L. cloustoni*. *A*, total ash in the stipes; *B*, total ash in whole plant; *C*, total ash in the fronds; *E*, laminarin in the fronds; *F*, laminarin in the whole plant.

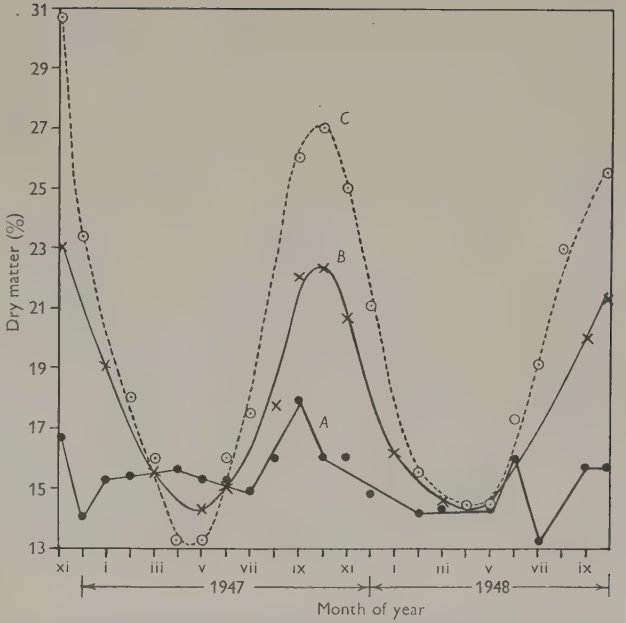

Fig. 2. Seasonal variation in dry matter in *L. cloustoni*. *A*, in the stipes; *B*, in the whole plants; *C*, in the fronds.

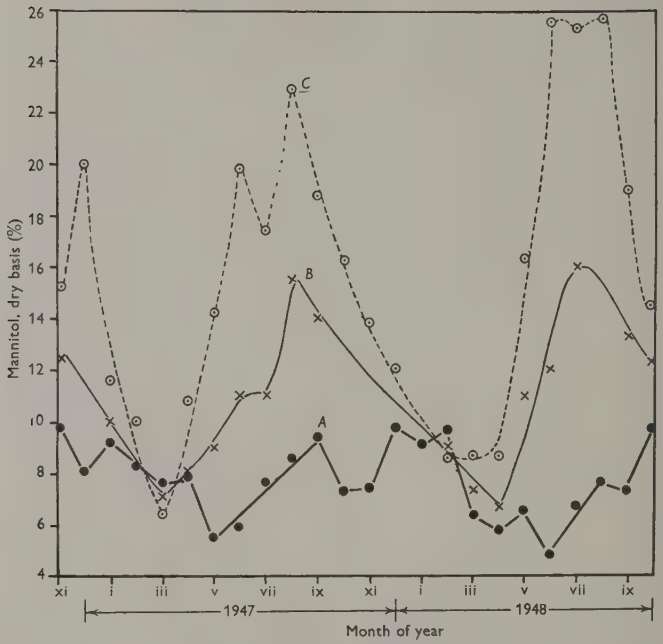

Fig. 3. Seasonal variation in mannitol in *L. cloustoni*. *A*, in the stipes; *B*, in the whole plant; *C*, in the fronds.

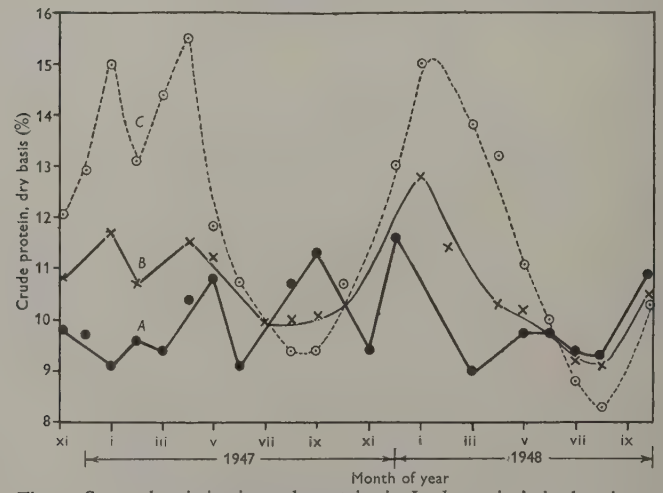

Fig. 4. Seasonal variation in crude proteins in *L. cloustoni*. A, in the stipes; *B*, in the whole plant; *C*, in the fronds.

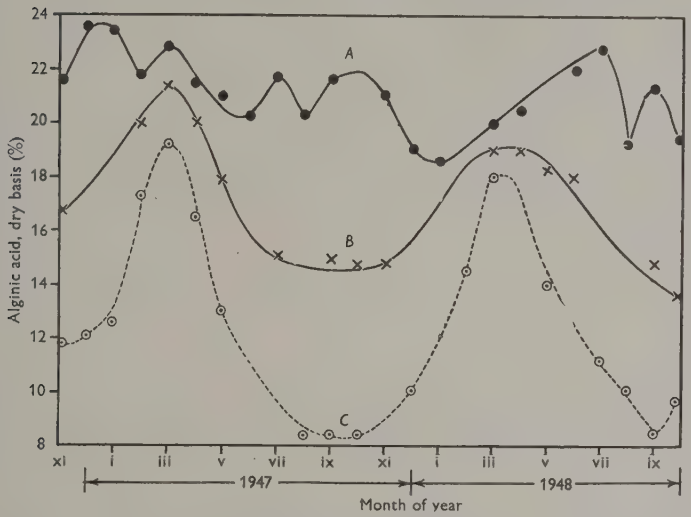

Fig. 5. Seasonal variation in alginic acid in *L. cloustoni*. *A*, in the stipes; *B*, in the whole plant; *C*, in the fronds.

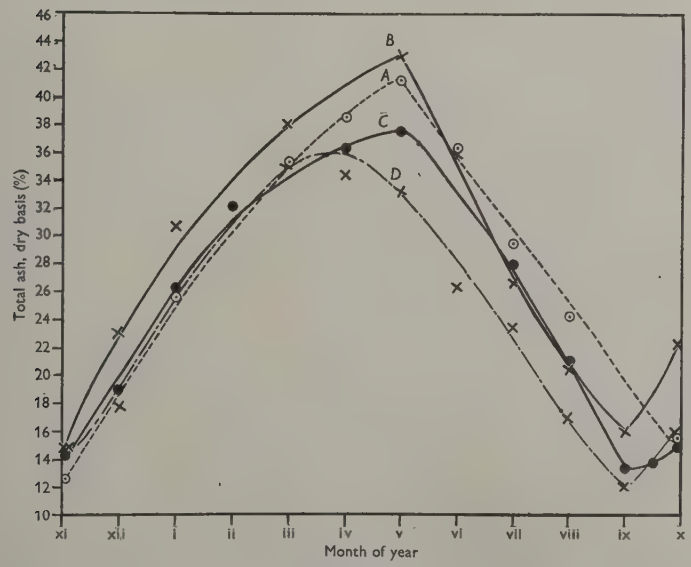

Fig. 6. Seasonal variation in total ash in *L. cloustoni* fronds. *A*, 1944–1945; *B*, 1945–1946; *C*, 1946–1947; *D*, 1947–1948.

reported has shown it to rise to 36% in December 1948–January 1949. No satisfactory explanation of this can be advanced. However, each month twenty plants of each species were weighed and the results indicate a progressive annual decrease in the weight of the plants.

Too much importance should not be attached to such figures, as the apparent weight reduction may only be due to the fact that repeated sampling from the same spot by means of a grapnel has progressively removed the larger and older plants.

	Nov. 1946 to Oct. 1947 Average weight of 240 plants (g.)	Nov. 1947 to Oct. 1948 Average weight of 240 plants (g.)
Frond	693	656
Stipe	1231	1141

Stipes

The stipes undergo slight seasonal variation, the ash being at a maximum in May (36–38%) and a minimum of 30% in November–December; in general, the variation follows that of the frond. The mannitol graph also shows seasonal variation but considerably less than that in the fronds, minima of 5% occurring in April–May and maxima of 9–10% in September–October. The dry weight content, however, shows very little variation (13–18%; Fig. 2).

The alginic acid shows no regular variation and fluctuates between 19 and 24%.

Laminaria digitata

Fronds

The outstanding difference between the fronds from Eilean Coltair (Loch Melfort) and Atlantic Bridge (open sea) is in the laminarin and dry-weight contents. Laminarin is absent for most of the year from the open-sea samples (Fig. 7), occurring only from July to October 1947 and from August to October 1948, the highest value being 15·6% in October 1948, as compared with 28% in the fronds from Loch Melfort and over 30% in *L. cloustoni* fronds. As previously stated, the environment at Atlantic Bridge favours the growth of giant plants and in consequence very little variation occurs in the dry matter content.

In the loch samples laminarin is absent from February to April, and reaches a maximum of 20% in September–October 1947 and 28% in October 1948, while the dry-weight content is at a minimum from January to March (11–12%) and a maximum in August–September (23–4%) in both 1947 and 1948.

The mannitol contents of the loch and open-sea samples are remarkably similar, and as with *L. cloustoni* the graphs are the inverse of the ash graphs (Figs. 9, 10). In general, the outstanding features are a temporary drop in mannitol and an increase in ash in July–August of 1947, and at the same period in the loch samples in 1948. A possible explanation of this is advanced in a recent publication (Black & Dewar, 1949).

The crude-protein graphs (Fig. 15) are very similar for loch and open-sea samples, exhibiting maxima of 12–14% between February and April and

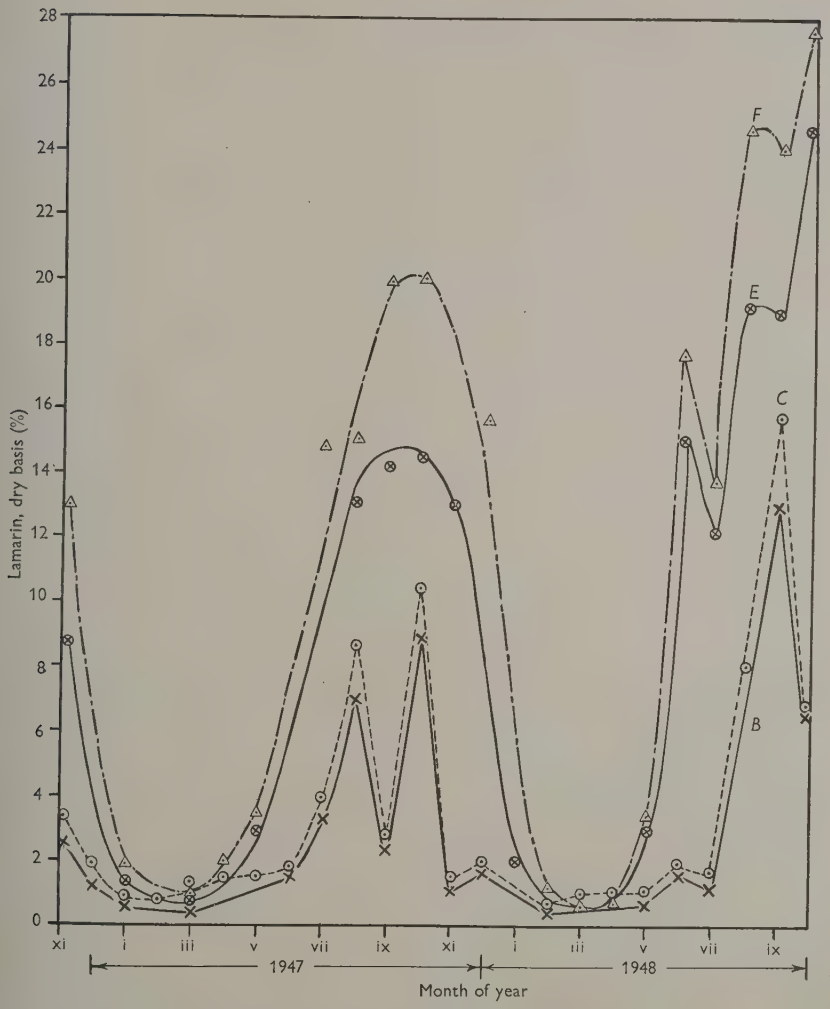

Fig. 7. Seasonal variation in laminarin in *L. digitata*. *B*, open-sea whole plant; *C*, open-sea fronds; *E*, loch whole plant; *F*, loch fronds.

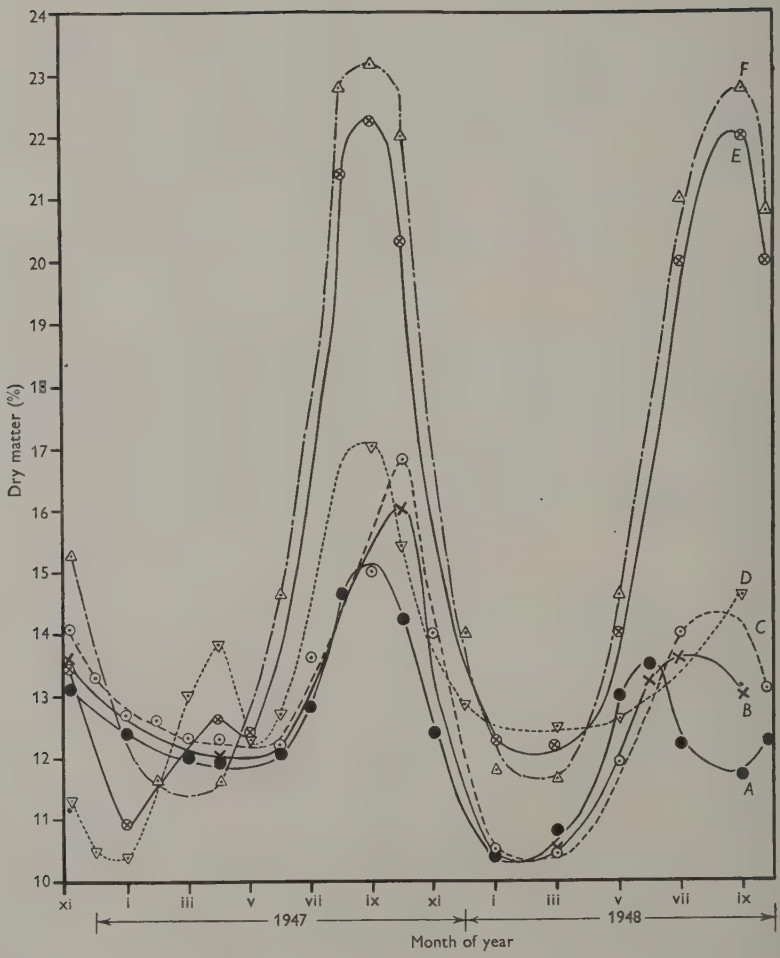

Fig. 8. Seasonal variation in dry-matter content in *L. digitata*. *A*, open-sea stipes; *B*, open-sea whole plant; *C*, open-sea fronds; *D*, loch stipes; *E*, loch whole plant; *F*, loch fronds.

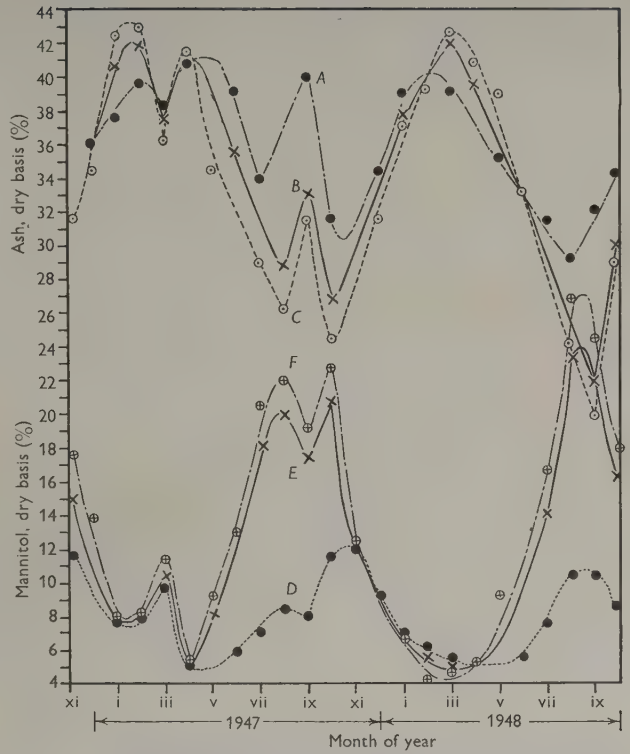

Fig. 9. Seasonal variation in ash and mannitol in *L. digitata* (open sea). *A*, ash in the stipes; *B*, ash in the whole plant; *C*, ash in the fronds; *D*, mannitol in the stipes; *E*, mannitol in whole plant; *F*, mannitol in the fronds.

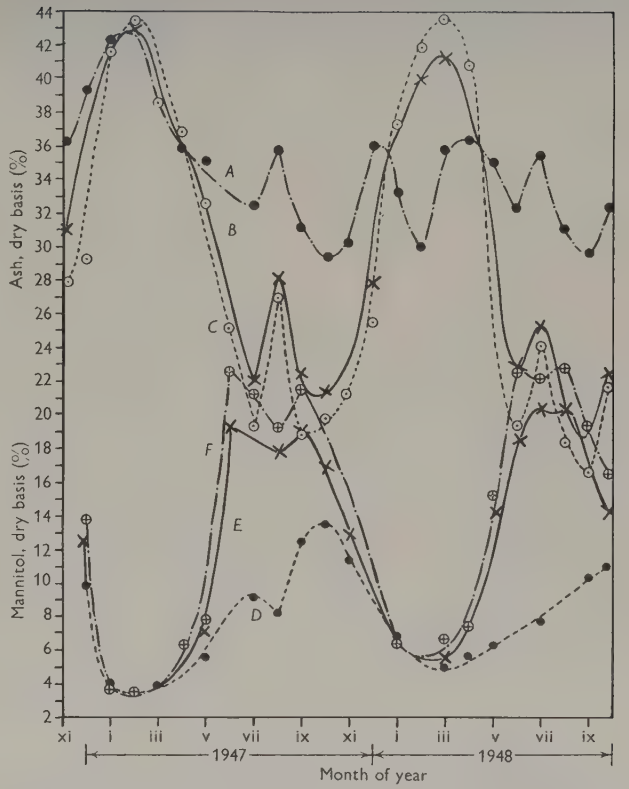

Fig. 10. Seasonal variation in ash and mannitol in *L. digitata* (loch). *A*, ash in the stipes; *B*, ash in whole plant; *C*, ash in the fronds; *D*, mannitol in the stipes; *E*, mannitol in the whole plant; *F*, mannitol in the fronds.

minima of 6–8% in the open-sea samples in August–October, and 4–6% in the loch samples at approximately the same time of the year.

The alginic acid graphs (Fig. 17) show that, in general, higher values are obtained for the open-sea samples, but this may be the result of the lower laminarin content as compared with the loch samples.

Stipes

In the stipes the composition follows fairly closely that of the fronds but the seasonal variation is within narrower limits.

Fronds · *Laminaria saccharina*

As with *L. digitata*, the main differences between the open-sea and loch samples are the higher laminarin and dry-weight contents of the loch samples. As conditions at Shuna Island, however, do not differ so much from Loch Melfort as conditions at Atlantic Bridge do, the open-sea samples of *L. saccharina* contain more laminarin than the samples of *L. digitata* from Atlantic Bridge.

The mannitol graphs for the open-sea and loch samples (Figs. 13, 14) are very similar and are again the inverse of the ash graphs. In the open-sea samples a temporary increase in mannitol and drop in ash occur in March 1947. A similar increase in mannitol occurs again in March 1948, but at this time of the year the shedding of the old frond and a rapid increase in photosynthesis influence the composition. In the loch samples a similar temporary increase in mannitol and decrease in ash occur in March 1947.

During the summer (June–August) of each year the characteristic temporary decrease in mannitol occurs.

The protein graphs (Fig. 16) for the open-sea and loch samples are remarkably similar, exhibiting maxima of 13–14% in February–March of each year, and minima of 5–6% in August–September with the exception of the open-sea samples which show a minimum of 8% in July–September 1947. In general, the loch samples show a higher concentration of proteins in the spring, and a lower concentration in the autumn, than the open-sea samples. The alginic acid graphs (Fig. 18) are also very similar, and for the greater part of the 2 years the graphs for the whole plants from the two localities actually coincide. Maxima of 19–20% occur in January–February of each year and minima of 11–12% in September.

The stipe graphs for all the constituents are in general parallel to those of the fronds.

A seasonal variation occurs in the fresh weight of the plants (Fig. 20) which is most marked for the fronds. Minima occur in January–February of each year and maxima in October, with additional maxima in July 1948.

In Fig. 19, the graphs for *L. saccharina* (loch), whole plant, are superimposed and give a complete picture of the changes in composition which occur during the 2 years.

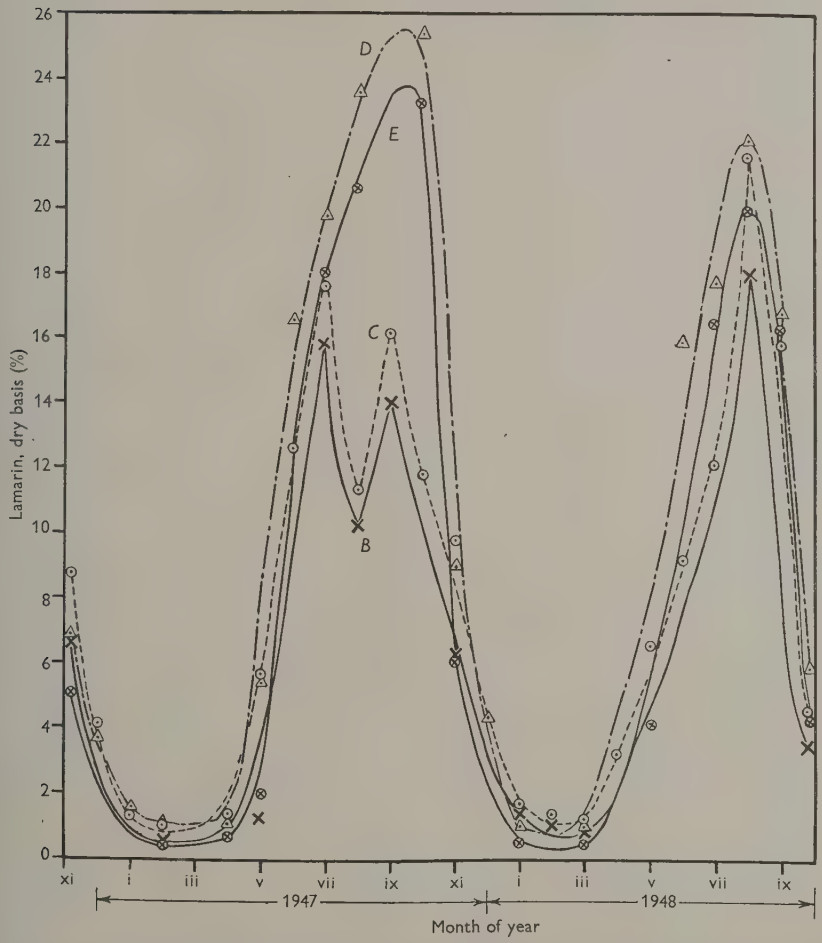

Fig. 11. Seasonal variation in laminarin in *L. saccharina*. *B*, in the open-sea whole plants; *C*, in the open-sea fronds; *E*, in the loch whole plants; *D*, in the loch fronds.

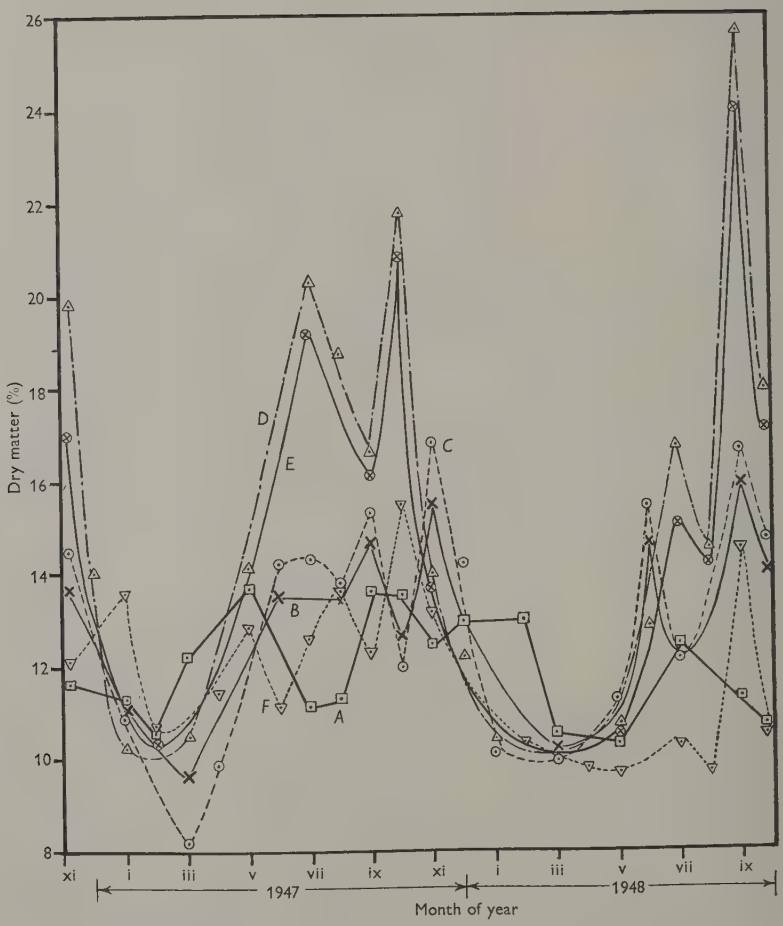

Fig. 12. Seasonal variation in dry matter in *L. saccharina*. *A*, in the open-sea stipes; *B*, in the open-sea whole plants; *C*, in the open-sea fronds; *D*, in the loch fronds; *E*, in the loch whole plants; *F*, in the loch stipes.

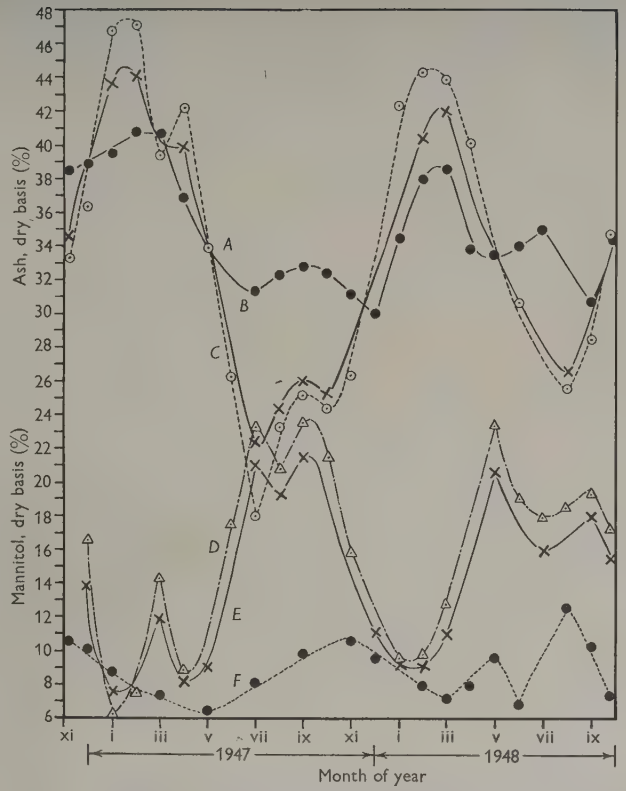

Fig. 13. Seasonal variation in ash and mannitol in *L. saccharina* (open sea). *A*, ash in the stipes; *B*, ash in the whole plant; *C*, ash in the fronds; *D*, mannitol in the fronds; *E*, mannitol in the whole plant; *F*, mannitol in the stipes.

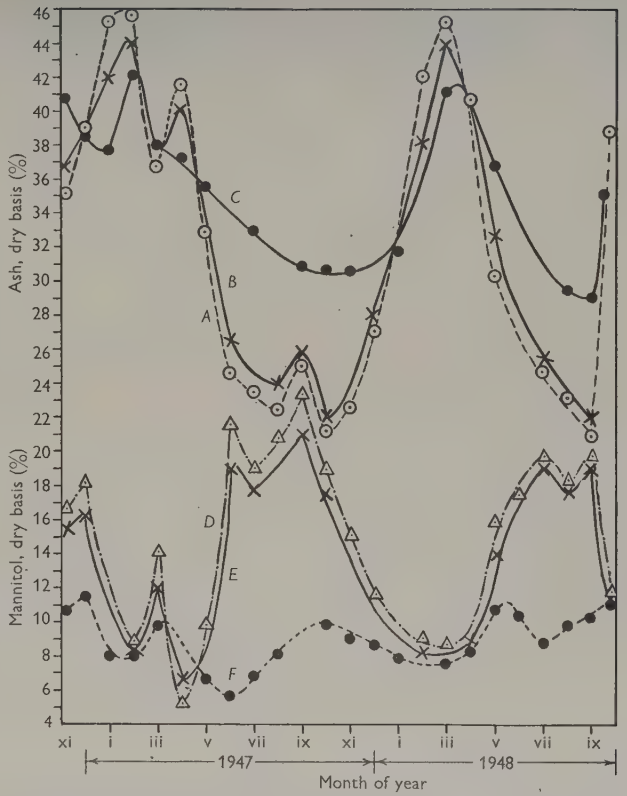

Fig. 14. Seasonal variation in ash and mannitol in *L. saccharina* (loch). *A*, ash in the fronds; *B*, ash in the whole plant; *C*, ash in the stipes; *D*, mannitol in the fronds; *E*, mannitol in the whole plant; *F*, mannitol in the stipes.

Preliminary Examination of the Haptera of the Laminarias

In Table III the composition of the haptera is compared with that of the stipe adjacent to it. With the exception of the *Nereocystis* stipe the haptera all contain a store of inorganic nitrogen which is absent from the adjacent stipes, and work at Jesus College, Oxford, by Young (private communication) has

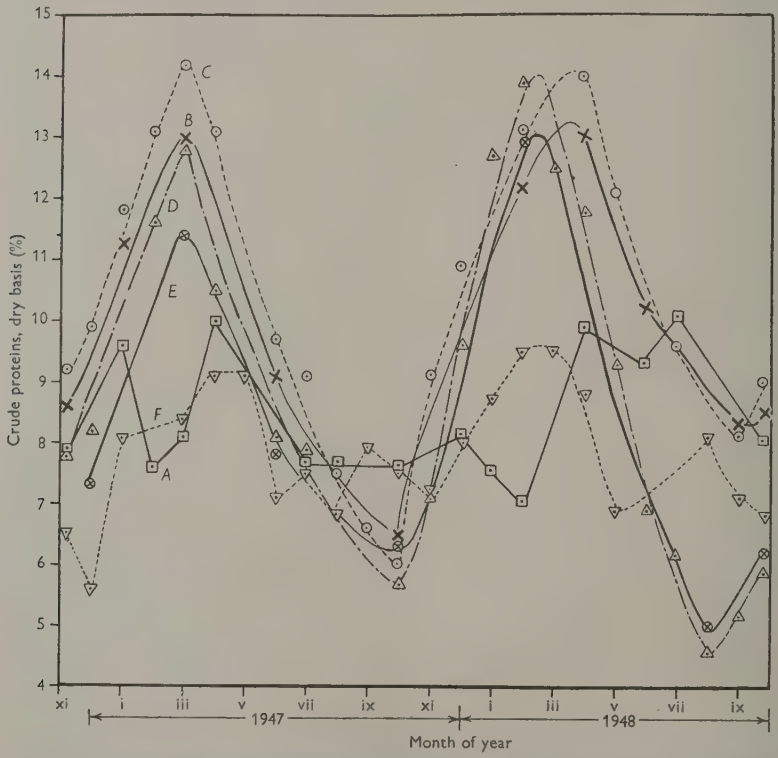

Fig. 15. Seasonal variation in crude proteins in *L. digitata*. *A*, open-sea stipes; *B*, open-sea whole plant; *C*, open-sea fronds; *D*, loch fronds; *E*, loch whole plants; *F*, loch stipes.

shown that the haptera contain a high percentage of free amino-acids. These results suggest the presence of growing tips in agreement with the result of Allsop (1948), who found an abundance of free amino-acids in actively developing tissue, but a low content in mature tissues not specially adapted for storage.

Parke (private communication) has confirmed that the haptera develop as

TABLE III. COMPOSITION OF THE HAPTERA OF THE LAMINARIACEAE *LAMINARIA CLOUSTONI*, *L. DIGITATA* AND *L. SACCHARINA*, AND *NEREOCYSTIS LUETKEANA* (DRY BASIS).

Sample	Date and place of collection	Total ash	Mannitol	Laminarin	Alginic acid	Crude proteins	Inorganic nitrogen
L. cloustoni, holdfast	July 1948, Cullipool	34·1	6·0	<1·0	6·6	14·0	0·17
L. cloustoni, stipe adjacent	July 1948, Cullipool	35·9	6·7	<1·0	22·9	9·4	Nil
L. digitata, holdfast	Oct. 1948, Atlantic Bridge	32·4	8·4	<1·0	18·8	15·3	0·20
L. digitata, stipe adjacent	Oct. 1948, Atlantic Bridge	34·2	8·6	<1·0	30·6	8·1	Nil
L. saccharina, holdfast	Oct. 1948, Shuna Island	37·3	7·4	<1·0	7·5	15·9	0·18
L. saccharina, stipe adjacent	Oct. 1948 Shuna Island	34·6	7·3	<1·0	24·9	9·1	Nil
N. luetkeana, holdfast	Oct. 1948, San Juan, Wash., U.S.A.	39·0	1·2	<1·0	6·9	16·3	0·41
N. luetkeana, stipe adjacent	Oct. 1948, San Juan, Wash., U.S.A.	40·8	1·2	<1·0	13·8	5·8	0·29

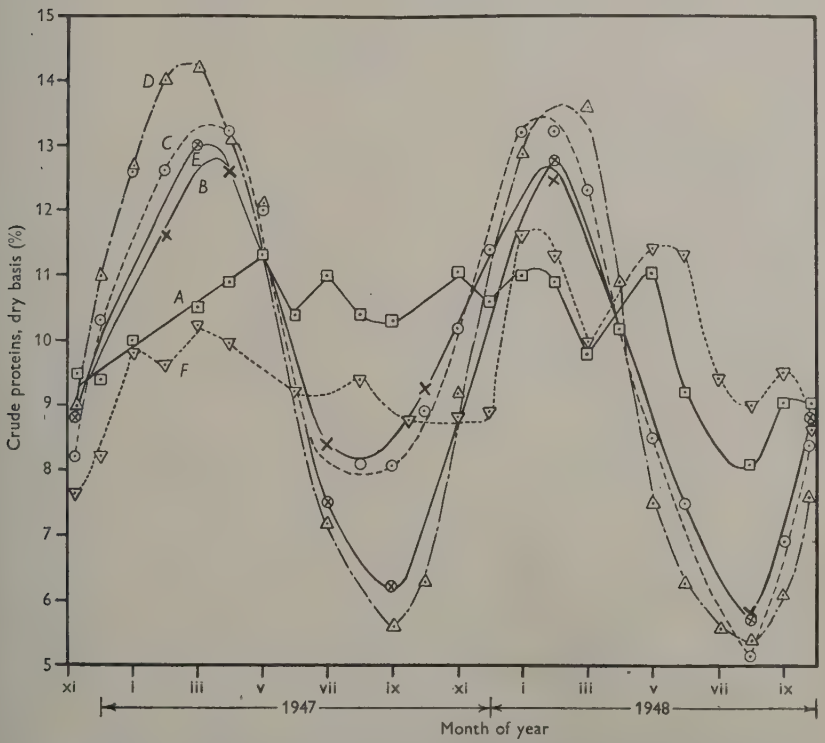

Fig. 16. Seasonal variation in crude proteins in *L. saccharina*. *A*, open-sea stipes; *B*, open-sea whole plants; *C*, open-sea fronds; *D*, loch fronds; *E*, loch whole plants; *F*, loch stipes.

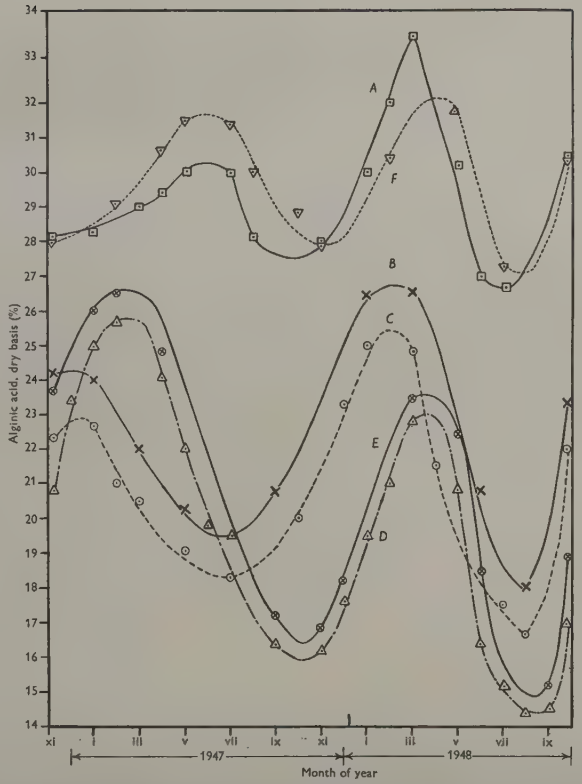

Fig. 17. Seasonal variation in alginic acid in *L. digitata*. *A*, open-sea stipes; *B*, open-sea whole plant; *C*, open-sea fronds; *D*, loch fronds; *E*, loch whole plants; *F*, loch stipes.

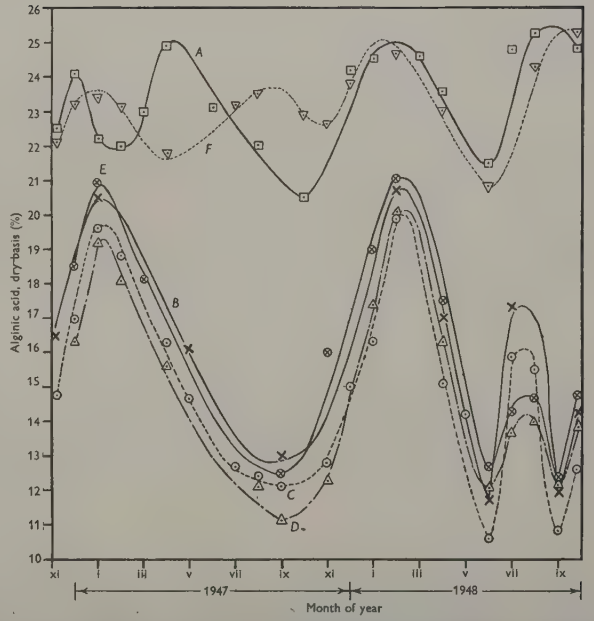

Fig. 18. Seasonal variation in alginic acid in *L. saccharina*. *A*, open-sea stipes; *B*, open-sea whole plant; *C*, open-sea fronds; *D*, loch fronds; *E*, loch whole plants; *F*, loch stipes.

outgrowths from a meristematic layer on the outside of the stipe, and once they start to form the tips can be regarded as growing tips.

It is interesting to note the low percentage of alginic acid, when determined by the standard method (Black, 1948). When the method was modified so that after soaking in acid the sodium carbonate was added without filtering off the

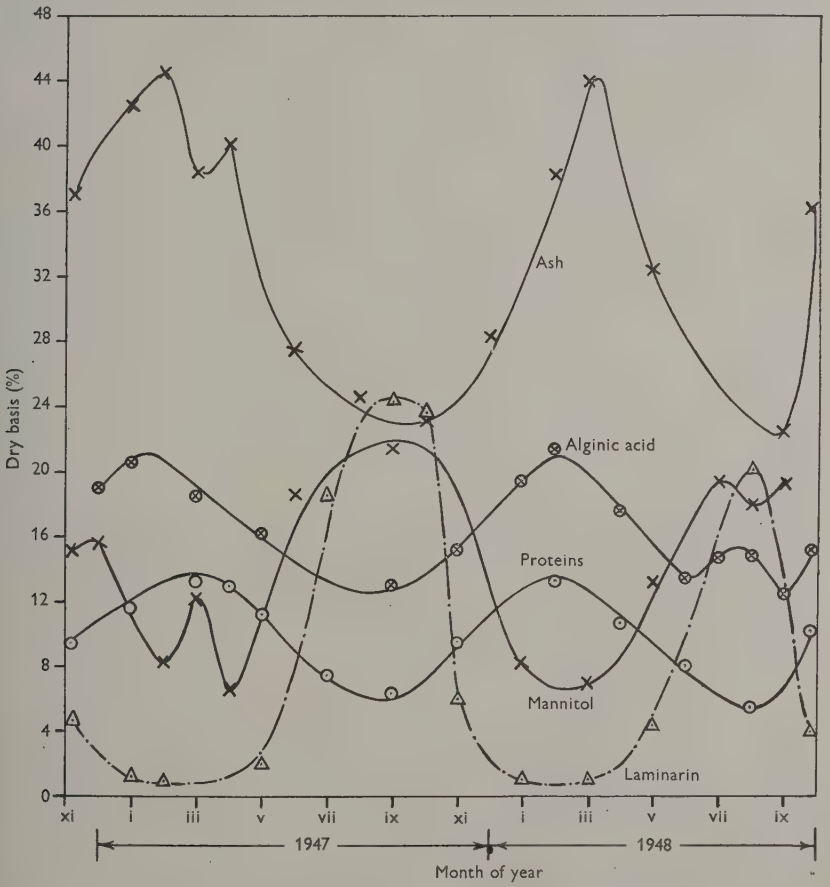

Fig. 19. Seasonal variation in *L. saccharina* (loch) whole plant.

weak acid solution, a result of 14·8% was obtained for the haptera of *Laminaria cloustoni*. When the alginic acid was determined by the carbazole method of Percival & Ross (1948*b*) a figure of 20·4% was obtained. The results indicate that in the haptera there is present either a water-soluble or a very low-grade alginate which requires further investigation.

The results show, however, that the haptera of *L. digitata* are considerably higher in alginic acid than those of *L. cloustoni* and *L. saccharina*, which may account for the very firm attachment which the holdfast of *L. digitata* has for the substratum.

The haptera as they touch the substratum become attached in a number of places. According to Parke (*loc. cit.*) they appear to secrete some sticky

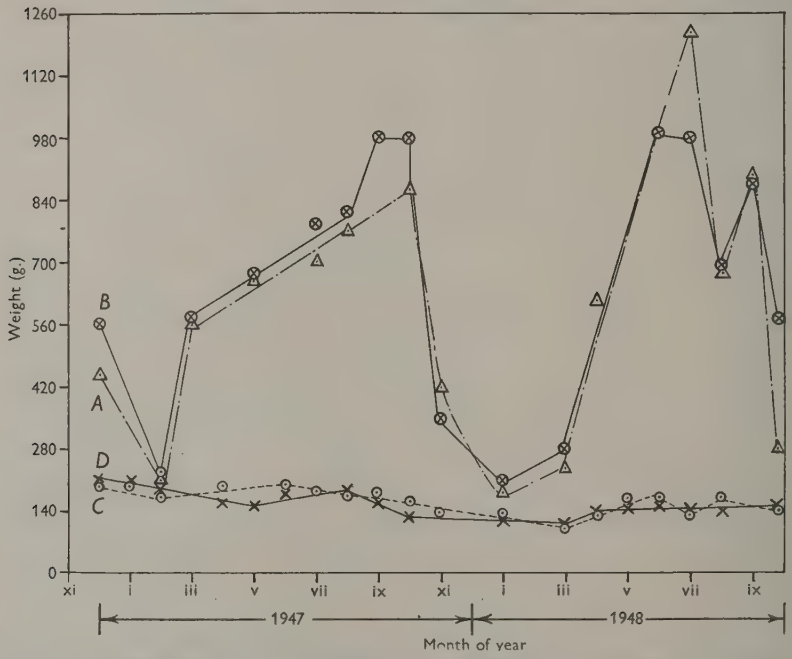

Fig. 20. Seasonal variation in fresh weight of *L. saccharina* in *A*, loch fronds; *B*, open-sea fronds; *C*, loch stipes; *D*, open-sea stipes.

substance which eventually appears as a hard chitinous layer. The low alginic acid content of the haptera, compared to the stipe, might indicate that an alginate is present in the mucilage which exudes, and there is the possibility that this alginate later becomes calcified and assists in cementing the haptera to the substratum.

Summary

The seasonal variations in the total ash, crude proteins, mannitol, laminarin and alginic acid contents are given for monthly samples of the Laminariaceae, *L. cloustoni*, *L. digitata* and *L. saccharina* from November 1946 to October

1948, samples of *L. digitata* and *L. saccharina* having been taken at different localities to determine the effect, if any, of the degree of exposure on the chemical composition.

The results agree favourably with those of the first 2 years examined and indicate that, with only a few exceptions, results might be reproducible in the corresponding season of any year, and it should be possible, therefore, to predict the approximate composition in subsequent years.

As before, the marked seasonal variations in chemical constitution occur in the fronds, where the bulk, if not all, of the photosynthesis occurs. The stipes undergo some variation parallel to that in the fronds, but within narrower limits, while laminarin is absent throughout the year.

In the fronds in the spring, mannitol is at a minimum and laminarin is absent, while the crude proteins, ash and alginic acid are at a maximum. In the autumn the reverse is true. The dry-matter content shows a corresponding variation, being at a minimum in the spring and a maximum in the autumn, but the variation is greatest in the loch samples and in *L. cloustoni* at Cullipool.

In the case of *L. digitata* and *L. saccharina*, the main effect of different degrees of exposure is that in the plants from the more sheltered localities (lochs) the laminarin and consequently the dry-weight contents are higher than in the more exposed samples, which might indicate 'restricted' growth in the lochs.

The fresh weight of the plants undergoes a similar seasonal variation, being at a minimum in the spring and a maximum in late summer.

A preliminary examination of the haptera has been carried out, and indicates a high inorganic nitrogen and free amino-acid content, while there is evidence of the presence of a lower grade alginate than is present in the adjacent stipe.

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A NOTE ON THE BARNACLE LARVAE OF THE CLYDE SEA AREA AS SAMPLED BY THE HARDY CONTINUOUS PLANKTON RECORDER

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In the course of an extensive series of tests on the Hardy Continuous Plankton Recorder (Hardy, 1939) carried out in the Clyde Sea Area during March and April 1949, a number of runs were made both during the time of the spring diatom outburst and over the period when barnacle larvae were a dominant feature of the zooplankton. It should be emphasized that the work was originally planned not as a plankton study but only as an investigation of the comparative performance of a number of recorders. Nevertheless, the limited data on cirripede larvae do give some quantitative information regarding the distribution and the total population of barnacle larvae over a moderately large area, and the quantitative relations of the stages, as well as providing some evidence bearing upon the hypothesis that the diatom outburst is a controlling factor in the development of the later stage larvae.

Since the results of these tests have not yet been published the following points regarding the performance of these recorders may be mentioned:

(1) The excellent depth-keeping properties of the machines have been fully confirmed; a constant depth of $10 \pm 0{\cdot}5$ m. was maintained over long distances by both machines under test.

(2) The amount of water filtered is probably the theoretical volume, since great increase in filtering surface (obtained by fitting large nets inside the machines) gave no significant increase in catch. This was true even with clogging which became apparent during the diatom outburst. It should, however, be remembered that the diatom was largely *Skeletonema costatum*; quantities of larger phytoplankton species could lead to incomplete filtration.

Thanks are due to Mr W. W. Brown who took part in the recorder investigations, to Mr M. W. H. Bishop for confirming the identity of the larval stages counted, and to Captain Stewart and the crew of the *Calanus* for their willing help in all the boat work.

The Collection and Counting of the Material

The plankton recorders were towed together in pairs under varying experimental conditions, and a statistical examination of the results has shown that in none of the tows here quoted was there any significant difference in the performance of the two machines. In Table I, therefore, only the mean catch

Table I. Cirripede Larvae from the Clyde Sea Area Population, Early Spring 1949; Total Catches and their Composition

Date	Run	Total catch cirripede larvae: Nauplii	Total catch cirripede larvae: Cyprids		The percentages stages, (i) *B. balanoides*, (ii) *B. crenatus* from subsample counts: Cyprids	VI	V	IV	III	II+I	Estimated numbers in original sample: Cyprids	VI	V	IV	III	II+I
21. iii. 49	2	1839	6	(i)	0·2	3·4	7·3	9·6	36·3	14·4	4	62	132	174	657	261
	3	1776	0	(ii)	0·6	1·1	7·3	5·2	7·8	1·6	11	20	132	94	141	29
	4	1418	5	(i)	0·9	4·6	16·4	14·5	34·6	17·3	13	66	233	206	492	246
				(ii)	0·0	3·3	2·3	1·4	1·9	1·9	0	47	33	20	27	27
	5	2230	14	(i)	0·2	5·1	16·4	19·3	29·9	9·2	5	114	368	433	671	207
				(ii)	0·1	4·6	5·3	3·4	2·1	0·7	2	103	119	76	47	16
22. iii. 49	6	1504	2	(i)	0·4	3·2	13·8	11·5	39·6	14·3	6	48	208	173	596	215
				(ii)	0·0	5·1	1·9	6·5	1·4	0·1	0	77	29	98	21	2
	7	1337	3	(i)	0·4	1·9	13·0	12·2	30·5	17·1	5	26	174	164	409	229
				(ii)	0·0	7·4	5·2	6·3	3·5	0·7	0	99	70	84	47	9
23. iii. 49	8	1848	10	(i)	0·7	3·3	12·8	24·1	34·8	11·1	13	61	238	448	647	206
				(ii)	0·0	1·9	1·9	2·2	1·4	0·1	0	35	35	41	26	2
	9	2886	27	(i)	0·2	2·8	12·7	27·8	28·7	5·7	6	82	370	810	836	166
				(ii)	0·0	6·4	5·3	5·3	1·7	0·2	0	186	154	154	50	6
	10	2959	27	(i)	0·2	2·6	7·5	27·5	24·2	10·1	6	78	224	821	723	302
				(ii)	0·4	5·2	4·2	5·4	6·3	2·1	12	155	125	161	188	63
	11	3633	46	(i)	0·3	3·0	8·6	24·1	24·1	9·6	11	110	316	887	887	353
				(ii)	0·8	7·5	5·3	8·4	5·1	1·1	29	276	195	309	188	40
4. iv. 49	12	2717	1888													
	13	2064	1472	(i)	26·9	19·5	8·7	4·5	1·4	0·7	895	649	289	150	47	23
	14	1650	1019	(ii)	10·0	5·3	5·6	1·9	0·6	0·3	338	176	186	63	20	10
	15	1326	1169													
5. iv. 49	16	1674	1475	(i)	42·8	10·9	4·8	1·6	0·6	0·1	1563	398	175	58	22	4
	17	2117	2036	(ii)	16·8	4·5	4·6	0·6	0·3	0·0	613	164	168	22	11	0

for the two machines on any given run is shown (columns 3 and 4). The recorders were run at their 'standard' depth of 10 m. The duration of each tow was half an hour at a speed of 8 knots (nominal), so that, neglecting the effect of tidal currents and wind, 4 nautical miles of water were filtered through the standard $\frac{1}{2} \times \frac{1}{2}$ in. nozzle, a total of 1·2 cu.m. of water per haul.

The area sampled extended from the north end of the Largs Channel to a point some 8 miles farther south, off the Little Cumbrae Island, the channel between the islands and the mainland being approximately 1 mile wide throughout this distance. The particular position of any run was not noted, the choice being dictated by considerations of convenience as regards the major project, namely the testing of the plankton recorders. The samples, therefore, although not random in the statistical sense, are probably representative of the conditions over this particular area.

For the purpose of all these tests the propellers of the machines were removed; in some the gauze remained stationary across the tunnel, whilst in others the inside mechanism was removed and a small net attached at the inner end of the fore part of the water tunnel. At the termination of each run the gauze both over the tunnel and for some distance on either side was cut out and, together with the catch, transferred to a breffit containing formalin; if a net had been used inside the recorder, it was carefully removed and the contents washed by means of a wash-bottle into a breffit.

The whole catch was first counted without sub-sampling, the barnacle larvae being recorded as nauplii and cyprids irrespective of stages or species; the mean catches per run for the two machines are shown in columns 3 and 4 of Table 1. The catches were then subsampled (some after pooling several samples) by Russell & Colman's technique (1931), and the number of the various stages of *Balanus balanoides* (Linn.) and *B. crenatus* Brug. counted in each subsample (one-tenth of the total catch). The percentages of these stages as determined from the counts of such subsamples are shown in columns 5–10. An estimate of the actual numbers of the various stages present in the original sample (single or pooled) was then calculated from these percentages and the mean value of the total number in the original sample or samples, and these estimates are given in columns 11–16.

The 'standard' gauze (60 mesh) was used in the recorders, and a microscopic examination of such gauze showed the holes to be approximately square and between 0·2 and 0·25 mm. in cross-section. Pyefinch (1948*a*) gives the full length of Nauplius I as 0·34 mm. in *B. balanoides* and 0·28 mm. in *B. crenatus*, while from his diagrams the carapace width of this stage in its widest part is slightly less than 0·25 mm. for the former, but only 0·15 mm. for the latter. Stage II of *B. balanoides* is given as 0·54 mm. full length and from the diagram 0·35 mm. carapace width, whilst Stage II of *B. crenatus*, which is rather more slender, is 0·44 mm. long and about 0·25 mm. greatest width. It would appear, therefore, that with the gauze used in these experi-

ments there is some chance that Nauplius I of both *B. balanoides* and *B. crenatus* and possibly Nauplius II of the latter were not caught quantitatively. It must, however, be remembered that the effective width of the animal is increased by the presence of appendages. Further, during many of these runs diatoms were very abundant, and considerable clogging of the gauze resulted; in these circumstances the effective opening of the gauze would be reduced and any loss of the earlier naupliar stages to some extent prevented.

The Weather and Hydrographic Conditions

During the course of all these collections and throughout the whole of the period covering the spring diatom outburst the weather was good. Winds, in general from the south-west, were moderate, the mean speed from 16th to 31st March being 10 m.p.h. The wind freshened during the first few days of April (19 m.p.h.). The daily surface sea temperatures (mean 7·53° C.) were rather higher than the average and varied only from 7·2 to 7·8° C. during this period, whilst the salinity, 31·5 °/₀₀, was normal for this period. The upper layers of the water at this time are homothermal, with consequent considerable vertical mixing, so that hauls at 10 m. may reasonably be considered as representative.

Table II

	1948–49 (° C.)	10-year mean (° C.)
November	10·6	10·1
December	9·4	8·4
January	7·9	7·3
February	7·4	6·6
March	7·2	6·9
April	8·2	7·2

In view of the extraordinary barnacle settlement, one of the heaviest for many years, it is of interest to record that throughout the winter and during the spring the sea temperatures (surface values) had been considerably higher than normal (Table II).

The Distribution of Larvae in Space and Time

The results set out in Table I indicate that over the whole area and over a considerable period of time the population of barnacle larvae showed no enormous fluctuations. Considering the catches of total larvae as separate samples of the larval population of the whole area sampled there is no significant difference between the means of the catches on the first 2 days (analysis performed on logarithmic values of catches), $t = 1{\cdot}568$, $n = 4$, $P = 0{\cdot}2$; there is a significant difference between the first two and the third day, $t = 3{\cdot}505$, $n = 8$, $P = 0{\cdot}02$–$0{\cdot}01$; but no significant difference between the third day and the last

2 days, $t = 1{\cdot}103$, $n = 8$, $P = 0{\cdot}3$. The mean for the first 2 days was 1689 larvae and the mean for the rest of the period was 3204 larvae.

The population and its composition over the area was remarkably constant on some of the days. Since each traverse extended 4 miles, the off-shore population even if made up of small swarms would be adequately sampled.

An analysis of variance for the first day, neglecting the cyprids since they were present in very small numbers, is given in Table III.

TABLE III

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects:			
Hauls (H)	2	0·2731	0·1366
Species (Sp)	1	3·4476	3·4476
Stages (St)	4	0·9311	0·2328
First-order interactions:			
H × Sp	2	0·1748	0·0874
H × St	8	0·5384	0·0673
Sp × St	4	0·7334	0·1834
Second-order interaction:			
H × Sp × St	8	0·3120	0·0390
Total	29	—	—

The mean square for H × Sp and H × St are not significant when tested against H × Sp × St. The values may be pooled giving a new residual of 0·0570 (18 degrees of freedom); and the value for hauls is not significant. There is therefore no significant difference between the hauls, and no significant difference between the proportion of species and stages in the hauls.

For the second day the analysis of variance is given in Table IV.

TABLE IV

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects:			
Hauls (H)	1	0·0433	0·0433
Species (Sp)	1	2·3318	2·3318
Stages (St)	4	1·0856	0·2714
First-order interactions:			
H × Sp	1	0·1868	0·1868
H × St	4	0·1126	0·0282
Sp × St	4	2·6738	0·6685
Second-order interaction:			
H × Sp × St	4	0·0659	0·0165
Total	19	—	—

Again H × St mean square is not significant, but at the 5% level the H × Sp mean square is significant. The value for the hauls is not significant. The proportion of the species therefore varied during the hauls, although the

proportion of the stages remained unchanged. However, on the third day, although H × St is not significant the value for H × Sp is high, indicating considerable variation in the proportions of the species in the hauls. The analysis of variance is given in Table V.

TABLE V

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects:			
Hauls (H)	3	1·8688	0·6229
Species (Sp)	1	4·0622	4·0622
Stages (St)	4	2·8604	0·7151
First-order interactions:			
H × Sp	3	0·8770	0·2923
H × St	12	0·4702	0·0392
Sp × St	4	2·5485	0·6371
Second-order interaction:			
H × Sp × St	12	0·2214	0·0185
Total	39	—	—

The wide day-to-day fluctuations often reported may be due to sampling techniques and also, particularly in respect of Stages I and II nauplii, to the effect of the abundant supply of parent stock when sampling is effected by nets attached to fixed inshore structures.

THE BARNACLE LARVAE POPULATION

It was found as a result of the present tests that in spite of such diatom clogging as was apparent at the time, the plankton recorders filtered the theoretical quantity of water. It is, therefore, possible to obtain an accurate estimate of the barnacle population, although such an estimate suffers from the disadvantage that nothing is known of the vertical distribution of the population.

The mean number of larvae per haul over the whole period is 2636 and this is taken in 1·2 cu.m. which gives 2197 larvae per cu.m. Pyefinch (1948*b*) gives 13,644 as the highest average daily haul for a single month. Now this figure was obtained with a 50 cm. net fished for 1 hr. under conditions which do not permit quantitative deductions. However, at a tidal speed of 1 knot the theoretical volume filtered is approximately 350 cu.m. of water per hour. Such a comparison suggests either that nets fished on the tide in this manner are not fishing effectively, or that the larval populations here recorded were very much higher than those previously recorded.

It is of some interest to calculate an approximate estimate of the total barnacle larvae population for the whole of this body of water. If it is assumed that the larvae were uniformly distributed down to a depth of 10 m., a reasonable assumption in view of the vertical mixing at this time of the year, and taking the area to be approximately 8 square miles and using the above value for the mean population density, the number of larvae is of the order of 6×10^{11}.

The Relation of the Stages

Pyefinch (1948*b*), Johnstone, Scott & Chadwick (1924), and Fish (1925) consider that between the Stages I and II Nauplii and the cyprid stage there is a considerable depletion of the population, although no cause is suggested. According to Pyefinch the interval between Nauplius III and the cyprid stage is of the order of 15–21 days. In the present instance such a developmental period would mean that all the barnacle larvae from Stage III to cyprids present in the first runs (21 March) should have appeared as cyprids by the time the run was taken on 5 April. Taking the *higher* population of the 23rd to represent this earlier stage of the population, the mean number of III to cyprid stages was 1894 and 580 for *B. balanoides* and *B. crenatus*, respectively. On 5 April the corresponding catches were 1563 and 614. This does not indicate any depletion of stock between Stage III and cyprid. It is possible that the depletion takes place between Stages I + II and III (on this point the data give no information), but it is suggested that the apparent depletion may be due to the fact that in taking samples off in-shore structures, as was done by Pyefinch and Fish, the numbers of Stages I and II are not representative of the planktonic content of the whole body of water. The catches of these two stages will be grossly influenced by the close proximity of the parent stock. It is also perhaps significant in this connexion, that Pyefinch found this discrepancy less for *B. crenatus*, a sublittoral species, and that his figures also show a much less discrepancy when the Stage III and cyprid populations are compared for *B. balanoides*. Johnstone *et al.* took their samples in the in-shore waters across Port Erin Bay and the proximity of parent stock may be partially responsible for the apparent discrepancy. Also it is to be noted that, according to the catches of these workers, there is a great increase in the diatom population at the time the cyprids were being caught; clogging of their nets may have resulted in the filtration of less water than was filtered when nauplii were the main larval stage present, under which circumstances more water would be filtered when the earlier stages were being sampled. Development takes place over a period of approximately 1 month, during which considerable dispersion of the larvae takes place (as indicated by the above results) so that the whole body of water should be sampled for the stages in order to compare any changes within the population. Further, the above results suggest that there is no reason to assume, as does Pyefinch, either that the cyprids tend to occur in greater numbers in-shore, or that they would become more abundant in in-shore waters later in the tide.

The Effect of Diatoms on the Larval Development

It has been maintained by Pyefinch (1948*b*) that the development of the later stages of the nauplii and the production of cyprids is considerably interfered with by a heavy diatom population. This does not seem to be true in the present series. On 16 March few diatoms were present, but the spring outburst of

Skeletonema costatum began between the 16th and 21st of that month, reached its maximum between the 22nd and 25th and was virtually over by the 31st. A lack of records does not allow speculation before the diatom outburst took place, but it is clear that development from Stage III to cyprids was never interfered with by the diatom outburst, since this is the period over which it has been shown that the earlier nauplii stages completed their development with the production of the 'corresponding' number of cyprids. That cyprid development took place is substantiated by the fact that settlement on the shore was first observed on 3 April (35–40 newly settled cyprids per sq.in.) and that there subsequently developed one of the heaviest settlements which has been seen in this area for a number of years. A non-toxic panel exposed on a raft in-shore during this period (in connexion with another investigation) and withdrawn on 15 April had 231 (mean of four separate counts) barnacles of less than 1 mm. in size per sq.in.

Summary

A series of results is presented on the barnacle larvae population of an area of the Firth of Clyde, over a 15-day period in the spring taken by means of a modified Hardy Plankton Recorder.

The records and observations on barnacle settlement indicate that the larval population was considerably greater than usual.

The total larval population showed no great fluctuations from day to day, and on a given day the composition of the population over a wide area was often reasonably constant.

Evidence is presented that there is no great depletion of the population between Nauplius III and cyprid stages. It is suggested that the depletion previously reported may be due in part to the method of sampling or to the conditions at the time of sampling.

During the time when the evidence indicates no depletion of population there was a heavy diatom outburst, which in this instance did not appear to interfere with the larval development.

Data are given on the density of settlement.

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OPHIOPSILA ANNULOSA (M. SARS) IN THE PLYMOUTH AREA

By H. G. Vevers, M.A., D.Phil.

Zoologist at the Plymouth Laboratory

Norman (1905) gave a short account of the distribution of the ophiuroid, *Ophiopsila annulosa*, having dredged it himself from Birterbuy Bay, Ireland, in 1874, and from outside Dartmouth Harbour in 1904. He also obtained specimens in 1903 from the Plymouth Laboratory; these had been dredged in 12–25 fathoms on Mewstone Ledge and Stoke Point Grounds, near Plymouth, and were recorded as not uncommon in the red sandstone, especially in old *Pholadidea* crypts. Mortensen (1927) expressed some doubt as to Norman's identification of the Irish specimens; he noted that the Plymouth specimens had been found in exactly the same locality and habitat as the smaller and commoner species, *Ophiopsila aranea*, and considered that the presence of the larger species in British waters could not be definitely settled until new records were to hand. *O. annulosa* was not recorded in the *Plymouth Marine Fauna* (Mar. Biol. Assoc., 1931) and no specimens have been found in the reference museum at the Laboratory.

On 8 July 1948 a single perfect specimen of *O. annulosa* was dredged by R.V. *Sabella* on the Mewstone Grounds in 20 fathoms. This specimen was not found in the crevices of the sandstone boulders, but came up loose in the dredge bag. A second specimen, for which I am indebted to Mr P. G. Corbin, was dredged on the Mewstone Grounds ($\frac{3}{4}$ mile south of the Mewstone, 18–20 fathoms) on 5 April 1949.

Furthermore, it has now been possible, through the courtesy of Dr H. W. Parker, to examine the specimens of *O. annulosa* in the Department of Zoology at the British Museum (Natural History). Three of the four specimens are from Norman's collections (viz. Birterbuy Bay 1874, Kenmare Bay 1877, and Zoological Station Naples 1887), while the remaining specimen was collected at Naples in 1948. These specimens undoubtedly belong to the same species as the specimens taken at Plymouth in 1948 and 1949. They were easily distinguishable from *O. aranea* Forbes, the marked brown and white banding of the robust arms and the large number of arm spines in *O. annulosa* being quite characteristic.

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THE OCCURRENCE OF THE SMOOTH SAND-EEL, *GYMNAMMODYTES SEMISQUAMATUS* (JOURDAIN), IN THE PLYMOUTH AREA, WITH NOTES ON *G. CICERELUS* (RAFINESQUE), AND *G. CAPENSIS* (BARNARD)

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Distribution and Plymouth Records of *Gymnammodytes semisquamatus*

Gymnammodytes semisquamatus (Jourdain), the smooth sand-eel occurring along the Atlantic seaboard of north-western Europe, has been separated by Duncker & Mohr (1939) as a distinct species from the Mediterranean smooth sand-eel, *G. cicerelus*[1] (Rafinesque). Until Raitt's discovery (1934, 1935) of the abundance of *G. semisquamatus*[2] in Scottish waters, only six specimens had been recorded farther north than the English Channel:

> Shetlands, one specimen as *Ammodytes siculus*, Günther (1867). Southern Norway, five specimens as *A. cicerellus*, Collett (1904), Grieg (1912). It has recently been identified by Poll (1947) from the West Hinder Bank in the southern North Sea (seventeen specimens, 15 May 1907). It does not occur in Swedish waters as stated in Corbin & Vati (1949, pp. 289–90) on Lönnberg's (1915) authority. When this was written it had unfortunately not been possible to consult Lönnberg (1915), and the error is a repetition of one occurring in Raitt's papers (1934, 1935).

The species has, however, long been known from the southern half of the mouth of the English Channel in the St Malo area, and along the Atlantic coast-line of France, Spain and Portugal, although not validly distinguished from *Gymnammodytes cicerelus* until the publication of Duncker & Mohr's study:

> St Malo area, as *Ammodytes semisquamatus*, Jourdain (1879), Moreau (1891). Atlantic coast, as *A. cicerellus*, France, Acloque (1900), Spain and Portugal, de Buen (1935), Gonçalves (1942).

Gymnammodytes semisquamatus was first identified in the Plymouth area in July 1947, and has since been taken during all months of the year.

It also occurs in the Irish Sea off the Isle of Man, a single specimen having been identified among a small part of the collection of the Marine Biological

[1] Dr E. Trewavas, British Museum (Natural History), has kindly pointed out that *cicerelus* is the original spelling of Rafinesque.

[2] Recorded as *Ammodytes cicerellus*, before Duncker & Mohr's separation of the two species.

Station, Port Erin, Isle of Man.[1] It was taken locally, although the date and precise place of capture were not recorded.

Raitt's records from Scottish waters, this single specimen from the Irish Sea, and the occurrence of the species in the Plymouth area indicate a continuous distribution from the Faroes, southwards along the west coast of Scotland, through the Irish Sea to the Western Channel mouth, joining thence with the previously known distribution along the Atlantic coast-line of France, Spain and Portugal.

The use of a trawl with a covered cod-end will, no doubt, reveal the species to be fairly widely distributed in the Irish Sea and Celtic Sea. It will be of interest to know whether it also occurs along the Atlantic coast of Ireland.

The following are the records from the Plymouth area:[2]

Twelve specimens were caught in the trawl on eight occasions (Mar. 1949, May 1949, June 1948 and 1949, July 1947, Aug. 1949, Sept. 1949). Forty-three specimens were taken by the dredge in shell gravel on seventeen occasions, once in Bigbury Bay and sixteen times from the Eddystone shell gravel (Jan. 1949, Feb. 1949, March 1948 and 1949, July 1949, Sept. 1948, Oct. 1947, Nov. 1947–9, Dec. 1948). Not infrequently, however, none has been caught during a day's dredging for *Amphioxus* on this ground. Ninety-six specimens were taken in six Agassiz trawl hauls on the Eddystone shell gravel (Feb. and Apr. 1949). This number is noteworthy since the Agassiz trawl can be towed for very little longer than 5 min. on this ground owing to its small area between the submerged long sharp reefs standing out from the main Eddystone Rock. Eight specimens were caught in a short trawl haul to the east of the Eddystone lighthouse, with the cod-end of the trawl covered with small mesh netting ($\frac{3}{8}$ in. bar), as used in the shell-gravel dredge and the Agassiz trawl (May 1949). One specimen was found in a whiting's stomach (Apr. 1949) and seven specimens in perfect condition were taken from the stomach of a turbot trawled to the south-west of Looe (May 1949).

Several observations may be made from these records. Before the present interest developed, the Agassiz trawl was seldom used on the Eddystone shell-gravel patch. Moreover, in the past, while sorting dredge hauls of shell gravel at sea, all attention was concentrated on securing *Amphioxus*; sand-eels, for which there was no special demand, are unlikely to have received the same attention. They are frequently damaged when caught in the dredge and may have been discarded for this reason, or, if brought in to the laboratory, were probably not closely examined. It seems reasonable then to infer that the species has previously been overlooked in the Plymouth area, and is not a recent arrival.

The infrequent captures in the trawl of very few specimens of *Gymnammodytes semisquamatus* reveal that the normal mesh size of the cod-end does not effectively retain sand-eels. This is amply borne out by the fact that the great

[1] The writer is indebted to Mr J. R. Bruce for kindly providing this material for examination.

[2] The writer's sincere thanks are due to Lieut.-Commander C. A. Hoodless, D.S.C., R.N.R., and Mr W. J. Creese, and to the members of the crews of R.V. *Sabella* and M.F.V. *Sula* for their constant watch for, and help in securing, specimens.

majority of Raitt's very large collection of Ammodytidae were caught while trawling with a small-mesh cover to the cod-end.[1]

The body form of a sand-eel and its ability to burrow in the dense medium of sand or shell gravel conceivably give it a greater chance than other 'trawl fish' of successfully escaping from the violent hurly-burly occurring in the cod-end of a trawl when fishing.

From the records of the area, it also appears that *G. semisquamatus* is an off-shore species with a preference for shell gravel grounds. Shore seining for sand-eels is commonly practised in many districts, but no specimens of *G. semisquamatus* have been seen during examination of a number of seine catches from Salcombe and the Exe estuary; in them *Ammodytes tobianus* was abundant, together with comparatively few *A. lanceolatus*. Nor has the species been taken by digging or hooking on the shore at several localities in South Devon and North Cornwall where both *A. tobianus* and *A. lanceolatus* were found.[2]

Although the actual numbers of *G. semisquamatus* caught in the dredge are low, they represent a considerable density of the species in the shell gravel in relation to the small volume of soil obtained by a dredge haul. The larger numbers caught by the Agassiz trawl on the shell gravel support this indication of a concentration, and it is further emphasized by the absence of *G. semisquamatus* from numerous Agassiz hauls made on other grounds in the Plymouth area including a number of 'control' hauls made close in to the Eddystone, but not actually on the shell gravel. The records of trawl-caught specimens show, however, that the species is not confined to the area of shell gravel. In relation to the above observations, the selectivity of the small mesh of the Agassiz trawl and the dredge must obviously be borne in mind. It is to be expected that more extensive use of a covered cod-end on the trawl will give fuller information on the distribution of the species.

A further point of interest is a seasonal alternation of the occurrence of trawled specimens (including those from the turbot and whiting stomachs) and dredged specimens. The occurrences are shown by months in Table I. Specimens caught by the Agassiz trawl and the small-mesh cod-end are not included since so few hauls were made with these nets.

It may be argued from the small number of records that this difference is fortuitous. On the other hand, the laboratory's two ships trawl throughout the year, and although not as frequent as trawling, dredging is necessitated by the constant demand for *Amphioxus*, whenever weather conditions are calm enough to work close to the Eddystone on the shell gravel. The seasonal difference

[1] Ascertained, by courtesy of Dr C. E. Lucas, from records at the Marine Laboratory, Scottish Home Department, Aberdeen.

[2] In the course of collecting, *Gymnammodytes semisquamatus* and *Ammodytes lanceolatus* have been taken together in the same haul. The characteristic lateral line of *semisquamatus* immediately distinguishes it. Although it has not been caught with *A. tobianus*, the same feature would also certainly distinguish it in this combination of species.

evident in Table I derives then from all-the-year-round sampling and in this event would appear to be a real one.

TABLE I. MONTHS IN WHICH *GYMNAMMODYTES SEMISQUAMATUS* HAS BEEN TAKEN IN THE PLYMOUTH AREA BY TRAWL AND DREDGE, JULY 1947 TO NOVEMBER 1949

Dredge	Trawl
Jan.	—
Feb.	—
Mar.	Mar.
—	Apr.
—	May
—	June
July	July
—	Aug.
Sept.	Sept.
Oct.	Oct.
Nov.	—
Dec.	—

There is thus a tentative indication of a winter concentration of the species in the shell gravel and a summer dispersal away from it. From examination of the gonad condition of the material, it would appear that the winter concentration in the shell gravel is associated with spawning. Very much fuller data are obviously necessary for confirming any of these indications; it is felt, however, that they are of some value in view of the lack of any knowledge about the life history of the North Atlantic smooth sand-eel.

THE NUMBER OF VERTEBRAE IN THE THREE SPECIES OF *GYMNAMMODYTES*

The number of vertebrae in *G. semisquamatus* from this area[1] is given in Table II for comparison with counts of specimens from Scottish waters (Corbin & Vati, 1949). There is very close agreement between the means of these two samples. Table II also contains vertebral counts of *G. cicerelus*, the Mediterranean smooth sand-eel. Previous vertebral-count data of the species (Fage, 1918; Duncker & Mohr, 1939) relate to a small number of specimens. The present sample of thirty-nine specimens (6·8–10·0 cm.) from the Naples area[2] is large enough to give a mean value, and it can be seen that this is not far removed from that of *G. semisquamatus*. It would be of interest to obtain further vertebral counts of *G. cicerelus* from other Mediterranean localities to examine whether there is extensive variation between different populations, as, for example, in *Ammodytes marinus* (see references in Corbin & Vati, 1949, Table II, p. 302), and in particular whether the vertebral number of the Black Sea population differs greatly from that of the Mediterranean population.

[1] The writer's sincere thanks are due to Surgeon-Commander D. R. F. Bertram, O.B.E., R.N., Royal Naval Hospital, Stonehouse, for the provision of beautifully clear X-ray plates of these specimens from which the counts were made.

[2] The writer is much indebted to Dr R. Dohrn, Director of the Stazione Zoologica, for this material.

Vertebral counts of fifty-nine specimens of the South African smooth sand-eel, *Gymnammodytes capensis* (Barnard, 1927), of 6·9–9·5 cm. length, are also included in Table II.[1] They were collected by R.R.S. *Discovery* in Elephant Bay, Angola, South Africa (Station 271, 29 July 1927, seine net, 5–0 m. depth). The wide difference between the vertebral counts of *G. semisquamatus* and *G. capensis* is remarkable in view of the extremely close similarity of external features in the two species. The specimens of *G. capensis* were very carefully compared with *G. semisquamatus* from this area and from Scottish waters, and it was found

TABLE II. THE NUMBER OF VERTEBRAE IN *GYMNAMMODYTES SEMISQUAMATUS*, *G. CICERELUS* AND *G. CAPENSIS*

No. of vertebrae (including urostyle)	*G. semisquamatus*		*G. cicerelus*	*G. capensis*
	Plymouth	Scotland		
57	..	..	..	5
58	..	..	..	23
59	..	..	..	22
60	..	..	..	9
61	..	..	..	..
62	..	..	..	..
63	..	..	..	..
64	..	..	..	..
65	..	1	7	..
66	2	1	17	..
67	15	10	13	..
68	43	20	2	..
69	33	15	..	..
70	13	4	..	..
71	1	..	..	..
72	1	..	..	..
Total no. of specimens	108	51	39	59
Mean vertebral no.	68·44	68·16	66·26	58·59
σ_{mean}	±0·098	±0·144[2]	±0·131	±0·113
σ	1·017	1·027[2]	0·819	0·857

that the two species could not be reliably distinguished by external features other than the numerical differences, noted by Duncker & Mohr (1939), of the number of fin-rays and the number of ventral pores in the lateral line. No differences of pigmentation were observed. Duncker & Mohr (1939) also distinguish *G. semisquamatus* and *G. capensis* by differences of the position of the tip of the pectoral fin and the end of the ventro-lateral skin-fold in relation to the line of insertion of the first ray of the dorsal fin. These differences could not, however, be confirmed in the above material. In the great majority of the *G. semisquamatus* and *G. capensis* examined, both the tip of the pectoral

[1] The writer is much indebted to Dr E. Trewavas, British Museum (Natural History), for the loan of the specimens for examination and of excellent X-ray plates from which the counts were made.

[2] Under *G. semisquamatus*, in Corbin & Vati, 1949, Table II, p. 302, the values of ±0·127 and 0·901 should be amended to read ±0·144 and 1·027 respectively.

and the end of the ventro-lateral skin-fold were in line with the insertion of the first ray of the dorsal fin; in some few specimens they extended very slightly beyond this line or were just short of it, by an interval of less than 1·0 mm. The interval in Duncker & Mohr's figs. 4*a* and 4*c* is considerably larger than this.[1] It is possible that there is some variation of these relative lengths with size, although no evidence of this was seen in the material examined. Nor, as these authors state, was the ventro-lateral skin fold of *G. capensis* observed to be less well developed than in *G. semisquamatus*. The external non-metameric differences between these two species appear therefore to be of little or no value for specific identification.

It may be added that, in the Mediterranean and Black Sea specimens of *G. cicerelus*, the tip of the pectoral extended slightly beyond (not more than 1·0 mm.) the line of the first ray of the dorsal. This is in agreement with Duncker & Mohr's description, although the pectoral is well short of this line in their fig. 4*b*[1].

Summary

Gymnammodytes semisquamatus, the North Atlantic smooth sand-eel, has a continuous distribution from southern Norway to the southern Atlantic coast-line of Spain. Its occurrence in the Irish Sea and in the Plymouth area are new records. In the latter area it is an off-shore species, apparently concentrating in shell gravel in winter for spawning. It has a mean vertebral number of slightly over 68 (Plymouth and Scottish specimens). A small sample of the Mediterranean species, *G. cicerelus*, gives a mean of just over 66, while the South African species, *G. capensis*, which is indistinguishable from *G. semisquamatus* by external non-metameric characters, has a much lower mean of 58·5.

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[1] Duncker & Mohr's (1939) fig. 4 is approximately natural size for adults of the three *Gymnammodytes* species.

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RECORDS OF PILCHARD SPAWNING IN THE ENGLISH CHANNEL

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(Text-fig. 1)

The pilchard, *Clupea pilchardus* Walbaum, is known to spawn in summer in the southern North Sea in the neighbourhood of the Sandettié Bank (Buchanan-Wollaston, 1911; Furnestin, 1939*a*, 1945) and in the eastern English Channel off Beachy Head (Furnestin, 1939*a*, 1945). Furnestin (1939*b*, 1945) concludes from these records that spawning is in all probability continuous throughout the Channel from the southern North Sea to the Celtic Sea. There appear, however, to be no previous references to pilchard spawning in the central part of the English Channel. The following records from the area are of interest therefore, and provide confirmation of Furnestin's conclusion.

The station positions and numbers per haul are shown in Fig. 1 and Table I. The plankton samples were collected in 1947 and 1948 by $\frac{1}{2}$ hr. oblique hauls of the 1 m. stramin ring-net during cruises of the motor yacht *Manihine*, which was placed at the disposal of the British Museum (Natural History) through the generosity of Major H. W. Hall, M.C. In 1948, a number of surface hauls with a medium silk townet were also taken by Mr M. H. W. Gall from his yacht *Colleen*. The writer is much indebted to the Trustees and Director of the British Museum for the opportunity of examining the *Manihine* collections, and to Mr Gall for the *Colleen* material.

A number of the *Colleen* stations (*C*1–12) were worked in the southern North Sea (see Gall, 1949, fig. 13, p. 772). Pilchard eggs were taken at four of these stations; at the northern entrance to the Straits of Dover (*C*9, Sandettié Bank; *C*10, south-east of Goodwin Lightship) and to the north-east off the Belgian coast (*C*7, north-east of Bligh Bank; *C*8, East Hinder Bank). None occurred at stations off the Norfolk coast (*C*1, *C*3 and *C*4) or close in to the Belgian coast (*C*5, *C*6 and *C*12). The presence of pilchard eggs in the area of the East Hinder and Bligh Banks slightly extends to the north-east the known spawning area of the species in the southern North Sea.

The *Manihine* stations, all of which were worked in the English Channel, fall into two groups; one to the west, the other to the east of the Isle of Wight. The monthly means of the numbers of pilchard eggs from all stations (positive and negative) of the two groups are given on p. 94.

Table I. Numbers of Pilchard Eggs, etc. per ½ hr. Oblique Haul of the 1 m. Stramin Net

* denotes figure obtained by subsampling.

Station number (date in parentheses)	Station position	Pilchard eggs (Mackerel eggs)	*Sagitta setosa* (*Sagitta elegans*)	*Muggiaea atlantica* (*Muggiaea kochi*)
	M.Y. Manihine			
23–25 July 1947				
1 (23)	50° 29′ N., 1° 41′ W.	200*	28 (22)	..
2	50° 20′ N., 1° 43′ W.	1	1 (2)	..
3 (24)	50° 39′ N., 0° 10′ W.	..	14 (3)	..
5	50° 19′ N., 0° 00′	123	..	..
6	50° 09′ N., 0° 05′ E.	147	..	..
7	49° 57′ N., 0° 07′ E.	4	..	..
8 (25)	49° 55′ N., 1° 54′ W.	..	..	..
9	50° 03′ N., 1° 51′ W.	68 (28)	..	..
10	50° 11′ N., 1° 47′ W.	38 (28)	..	..
27–28 August 1947				
11 (27)	50° 26′ N., 0° 25′ E.	97	8	..
12	50° 27′ N., 0° 29′ E.	3	5	..
13	50° 20′ N., 0° 37′ E.	..	..	..
14	50° 13′ N., 0° 46′ E.	..	..	..
16 (28)	50° 47′ N., 1° 10′ E.	..	1	..
17	50° 35′ N., 1° 20′ E.	1	3	..
18	50° 03′ N., 1° 37′ E.	..	1	..
6–7 May 1948				
†19 (6)	50° 39′ N., 0° 39′ E.	4980*		
†20	50° 53′ N., 0° 53′ E.	2468*		
21	50° 47′ N., 1° 10′ E.	1980*	..	..
22	50° 38′ N., 1° 24′ E.	9	..	..
24	50° 13′ N., 0° 46′ E.	3	1	..
25 (7)	50° 36′ N., 0° 26′ E.	8680*	1	..
26	50° 27′ N., 0° 29′ E.	480*	..	..
27	50° 20′ N., 0° 39′ E.	440*	..	..
15 June 1948				
33	50° 40′ N., 0° 11′ W.	800*	2	..
34	50° 27′ N., 0° 18′ W.	600*	..	..
35	50° 18′ N., 0° 02′ W.	260*	13	..
36	50° 09′ N., 0° 05′ W.	820*	2	..
37	50° 00′ N., 0° 00′	660*	..	..
3–4 July 1948				
40 (3)	50° 29′ N., 1° 42′ W.	800*	..	..
41	50° 20′ N., 1° 39′ W.	62	..	..
42	50° 11′ N., 1° 45′ W.	479 (21)	..	..
43 (4)	49° 54′ N., 2° 10′ W.	29 (54)	4	..
44	49° 51′ N., 2° 18′ W.	.. (10)	8	..
45	49° 54′ N., 1° 55′ W.	44 (12)	..	..
31 August 1948				
47	49° 55′ N., 2° 08′ W.	..	128	.. (2)
48	49° 52′ N., 2° 10′ W.	..	168	.. (2)
49	49° 50′ N., 2° 08′ W.	..	72	..
50	49° 49′ N., 2° 28′ W.	..	23	1 (8)
51	49° 50′ N., 2° 21′ W.	..	2	3 (7)
15, 26 September 1948				
52 (15)	50° 06′ N., 3° 27′ W.	..	207 (1)	96 (21)
53	50° 00′ N., 3° 16′ W.	..	1000*	61 (11)
54	49° 51′ N., 3° 07′ W.	..	500*	93 (37)
57 (26)	50° 31′ N., 1° 25′ E.	2	10	..
58	50° 38′ N., 1° 26′ E.	20	13	..
59	50° 47′ N., 1° 07′ E.	8	1	..
	Yacht *Colleen*‡			
*C*1 (15. vii. 48)	52° 28′ N., 1° 47′ E.	..		..
*C*3 (16)	52° 43′ N., 2° 18′ E.	..		..
*C*4 (19)	52° 26′ N., 2° 24′ E.	..		..
*C*5 (23)	51° 51′ N., 3° 38′ E.	..		..
*C*6	51° 55′ N., 3° 29′ E.	..		..
*C*7 (24)	51° 48′ N., 2° 58′ E.	76		..
*C*8	51° 36′ N., 2° 41′ E.	33		..
*C*9 (25)	51° 12′ N., 1° 54′ E.	8		..
*C*10 (29)	51° 11′ N., 1° 39′ E.	11		..
*C*12 (30)	51° 11′ N., 2° 41′ E.	..		..
*C*13 (5. viii. 48)	50° 46′ N., 1° 34′ E.	..		..
*C*16 (14)	50° 36′ N., 0° 03′ W.	4		..
*C*17 (15)	50° 21′ N., 0° 34′ W.	..		..
*C*19 (16)	49° 45′ N., 1° 00′ W.	..		..
*C*20 (20)	2 mls. N. of Alderney Lt. House	1		..
*C*21 (21)	50° 23′ N., 1° 51′ W.	..		..
*C*22 (24)	50° 16′ N., 1° 33′ W.	..		..
*C*23	50° 07′ N., 2° 21′ W.	..		..
*C*24 (6. ix. 48)	50° 04′ N., 4° 22′ W.	..		..
*C*25	49° 56′ N., 3° 47′ W.	..		1 numerous eudoxids
*C*26 (9)	49° 47′ N., 2° 01′ W.	..		..
*C*27 (10)	49° 56′ N., 1° 47′ W.	..		..
*C*28 (11)	50° 11′ N., 1° 33′ W.	..		.. (1) numerous eudoxids

† The writer is indebted to Mr A. C. Simpson, Fisheries Laboratory, Lowestoft, for the counts of pilchard eggs from these two stations.

‡ Catches not examined for mackerel eggs and *Sagitta* spp.

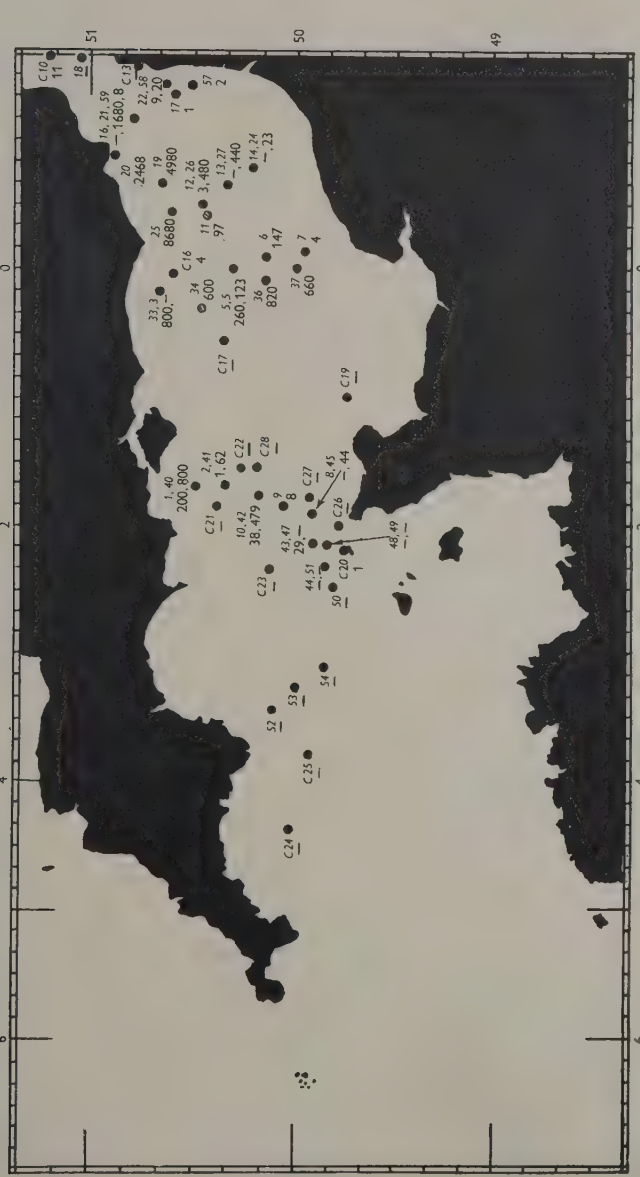

Fig. 1. Records of pilchard spawning in the English Channel in 1947 and 1948. Station numbers are shown in italics. The lower figures are the numbers of pilchard eggs per haul. Stations worked by the *Colleen* have the prefix *C*; those worked by the *Manihine* have no prefix. Several of the stations which were close together have for convenience been indicated by a single point on this chart.

In order roughly to compare the intensity of spawning in the central English Channel with that of the Celtic Sea (Corbin, 1947),[1] the means of the present records have been multiplied by four (figures in parentheses) to approximate the 1 m. net catches to those of the 2 m. ring-trawl. It should be noted that

Western stations			Eastern stations		
			May 1948	2379	(9516)
			June 1948	628	(2512)
July 1947	61	(244)	July 1947	68	(272)
July 1948	236	(944)			
Aug. 1948	Nil		Aug. 1947	14	(56)
Sept. 1948	Nil		Sept. 1948	10	(40)

the Celtic Sea spawning intensities were calculated from positive stations where more than 100 eggs per haul occurred. A detailed quantitative comparison of the two areas would require more comprehensive sampling in the English Channel. It should be further noted that the duration of some of the *Manihine* hauls varied considerably.

Data of the numbers per haul of mackerel eggs, *Sagitta* spp. and *Muggiaea* spp. are included in Table I, as they are complementary to the observations on the abundance of these species in Plymouth off-shore waters.

The small numbers of mackerel eggs taken in the central Channel in July 1947 and 1948 are in agreement with the low intensity of spawning observed in July 1937 and 1938 at the western entrance of the Channel (Corbin, 1947).

In autumn 1948, *Muggiaea atlantica* and *M. kochi* were plentiful off Plymouth (Corbin, 1949), and the present records show that both species were distributed up Channel to about 2° 30′ W. (St. 51), with *M. kochi* extending slightly farther eastwards to about 1° 30′ W. (St. *C*28) and also out-numbering *M. atlantica* at the easterly stations.

The absence of *Sagitta* spp. in July and August, 1947, in May–July 1948, and their presence in small numbers in August and September 1948, agrees with the Plymouth records (Corbin, 1948, 1949). In the eastern Channel, *S. elegans* occurred at one station only (St. 3, off Beachy Head, three specimens).

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[1] The writer wishes to correct an error which occurred in this paper. In the last line of Table III, page 81, the mean 1937–39 intensities of pilchard spawning should be amended to read: April 6680, May–June 14,843, July 4701.

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ON THE PRODUCTION OF LIVING MATTER IN THE SEA OFF PLYMOUTH

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(Text-figs. 1–10)

CONTENTS

	PAGE
The phytoplankton	98
Methods of estimation	100
The standing crop of phytoplankton	104
The annual production of phytoplankton	106
Factors affecting the annual production of vegetation	108
The zooplankton community	112
Food of the zooplankton	116
Fluctuations in population density	120
Pelagic fish	122
Bacteria in suspension	124
Demersal fish	125
The bottom fauna	126
Bacteria in the sea floor	128
On the quantity of organisms present, and their daily food requirements	129
Evidence of changing fertility	132
Bibliography	136

A study, now in progress, of the phosphorus cycle in the sea off Plymouth required some knowledge of the amount of plants and of several ecological groups of animals. There were no existing data except for zooplankton and the larger net-caught phytoplankton.

From information supplied by friends and colleagues, it was possible to make tentative estimates of the average biomass of other groups of animals occurring below unit area of the sea.

Although some of these estimates are derived indirectly and are indeed tentative, together they provide a framework on which to compute the food supply and food requirements of the animal population. There results a picture, crude and in part indefinite, of the quantitative relations between the different ecological groups and of how change of circumstance may affect the populations. It is the aim of this essay to present this picture.

The help of many friends and colleagues is gratefully acknowledged, both in supplying information and in amending drafts of this essay. To Mr P. G. Corbin and Mr P. S. B. Digby, who collected, sorted and weighed hauls of plankton in June 1947, and to Dr L. H. N. Cooper, who collected many samples for me, I am further indebted.

The Phytoplankton

The great difference in size of the various species which make up the community in these seas is perhaps more striking than the diverse shape of the different species.

	Contents, sap and tissue (cubic microns)
Diatoms	20–20,000,000
Dinoflagellates	500–100,000
Flagellates	14–500
Coccolithophores	14–500

Even among individuals of the same species, notably in species of diatoms, there are very considerable differences in size. Thus a large individual of *Ditylum Brightwellii* may have a volume of one to two million cubic microns and a small individual of fifty thousand—a thirty-fold difference in size within the same species.

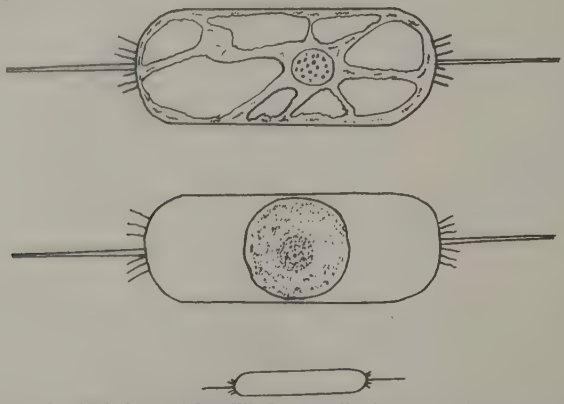

Fig. 1. Cells of *Ditylum Brightwellii*. Large cells about 90 μ diameter, small cell 15–20 μ diameter. (After Gross, 1937.)

Normally these plants are considered in terms of their linear dimensions; but the cubic dimensions of their cell contents will give a better measure of each individual's value as food for other organisms.

In some species the cells appear well filled with living tissue; in other species there is more sap than tissue. Thus, in *Ditylum*, the protoplasm normally lines the inside of the cell and projects as a network through the watery sap. It readily responds to stimulus, such as a fall in temperature, by rounding into a ball. It is then seen to occupy only a quarter of the cell content.

Given a suitable intensity of light, and a sufficient supply of dissolved nitrogen and phosphorus compounds in forms which they can absorb, these plants are capable of very rapid growth. Thus, Braarud (1945) has observed that some of the smallest plants double in numbers every 5 hr., while larger

species required 10–75 hr. The optimum light intensity and temperature also differ for different species.

One of the earliest and most illuminating experiments on the rate of growth was made by Gaarder & Gran (1927) in the following manner. Water was collected on 22 March from Oslo Fiord, the population density of the dominant species determined, and the water then put into flasks which were hung at different depths in the fiord. The temperature was 1·8° C. After 3 days, on the 25th, the population density was again determined.

	Percentage increase in 24 hr.		
Depth (m.)	*Lauderia glacialis*	*Thalassiosira gravida*	*Thalassiosira Nordenskioldii*
0	77	59	10
2	79	58	73
5	70	55	67
10	28	34	23
20	0	0	0

Compared with conditions in the English Channel at the end of March, this fiord water is 6–7° C. colder, less transparent, but richer in nutrient salts. It is notable that optimum growth took place in the upper 5 m., whereas off Plymouth and the Firth of Clyde in summer the optimum probably lies at about 10 m. depth, due to greater transparency of the water.

Several experiments have shown that if water is collected off Plymouth at about this season of the year, and kept at room temperature in a flask in a north window, where the intensity of light is similar to that at some 10 m. depth in the sea, the plant cells proliferate and use up the available nutrient salts within a few days. If the nutrient salts are increased ten-fold and the water is kept aerated, within about 14 days they are all utilized by the plants and a crop is produced having the same species constitution, but very many times denser, than that which appears in the sea at the time of the phytoplankton maximum. In some experiments it was found necessary also to add iron in an available form in order to ensure complete utilization of the nutrients.

Another characteristic of these unicellular plants is their high proportion of protein and fat when their organic content is compared with that of land plants. Various analyses of marine diatoms collected from the sea show 30–40% of protein and 7–10% of lipoids in their tissue. Recent analyses by Ketchum & Redfield (1949) of a number of unicellular algae, mostly fresh water, grown in artificial light, showed that composition of their organic matter was surprisingly similar: protein, 41–54%; carbohydrates, 20–38%; lipoids, 20–27%.

These algae were grown in water containing a plentiful supply of available nitrogen and phosphorus, and of carbon dioxide. Under conditions where either available nitrogen was deficient or both nutrients were deficient, the plants contained a smaller proportion of protein.

These various analyses show that marine phytoplankton has a remarkably high food value for animals. The protein content of the plants and the rapidity with which they can grow are outstanding features.

Methods of estimation

Owing to the great difference in size of the individual organisms comprising the plant community, it is a matter of practical difficulty to determine the population density or standing crop of plants per unit area of the sea. Catches made by net, either hauled vertically through the whole column of water or towed horizontally at various depths, collect a proportion of the organisms—a proportion which varies greatly with time and position. Concentration of the plants in a sample of water, by sedimentation, centrifuging, or by filtration through a membrane, and counting the individuals has been extensively employed. In order to arrive at the quantity or volume of plant tissue in the organisms, measurements of individuals, often of complicated shape, are needed, and small errors in linear measurements cause large errors in the estimate of volume. Moreover, the proportion of plant tissue in cells containing vacuolar sap is difficult (or even impossible) to gauge. Counting and measurement require much time. Unless the results can be expressed in terms of quantity of plant tissue they do not give a direct measure of the food value of the standing crop to the animal dependent on it for food.

In order to obtain the numerous observations necessary to assess the ever-changing crop, an indirect method has been rather extensively employed. The approximate quantity of chlorophyll in the plants can be quickly determined; it does not provide a direct linear measure of the organic matter in the plants, but it is perhaps as good an overall measure as could be obtained by any other method and allows numerous observations. In addition to providing a rough measure of the vegetable organic matter, experiments by Gessner indicate that it provides a direct measure of the capability of the plants to produce organic matter. He kept waters from a number of Bavarian lakes, having different phytoplankton floras, in the same light intensity at the same temperature. The quantity of chlorophyll in the phytoplankton showed a near relation to the assimilation which took place in unit time in the water from eleven lakes out of thirteen (Fig. 2). Hence the quantity of chlorophyll in the water gives a measure of the capacity or potentiality of the plants contained in it to produce vegetable food for the animal population.

In using chlorophyll determinations to compute the quantity of vegetable organic matter in the sea, two operations are involved which need consideration—there is the technique of estimating the chlorophyll in the plants filtered from a sample of sea water, and, having determined the quantity of chlorophyll in the plants below a unit area of the sea, there remains how best to gauge from it the quantity of vegetable tissue in which it had existed.

Chlorophyll occurs in algae as a mixture of chlorophyll *a* and chlorophyll *c*

(chlorofucin), always in conjunction with carotinoid pigments, largely fucoxanthin. The yellow carotinoids and the green chlorophylls leach out from the plants into 80% acetone, or into alcohol. Whichever solvent is used, substantially the same depth of green colour results, and this green colour has the same tint or hue whether it is extracted from diatoms, fucoid sea weeds or a common golden brown flagellate. Hence the proportion of chlorophylls to carotinoids is similar.

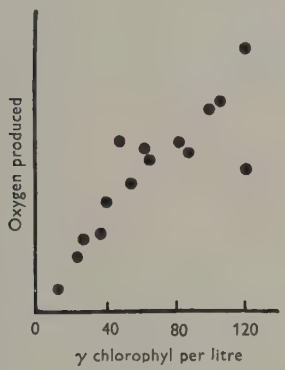

Fig. 2.

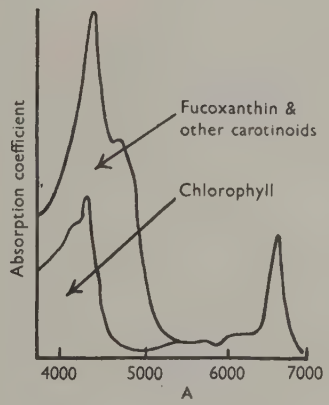

Fig. 3.

Fig. 2. Relation between assimilation and chlorophyll content of waters from thirteen Bavarian lakes. (After Gessner, 1943.)

Fig. 3. Absorption spectra in acetone of the pigments in the diatom *Nitzschia closterium*. (After Dutton & Manning, 1941.)

In consequence, these extracts can be matched visually against a stable and reproducible green standard solution. This is more yellowish green than a solution of pure chlorophyll; it can be evaluated against chlorophyll solution to which a yellow has been added to assist colour matching. To do this exactly would entail a pure preparation of chlorophylls *a* and *c* in the proportion in which they occur in algae. It is not necessary for our purpose to express the colour in terms of chlorophyll concentration because the depth of yellow-green colour in the extract is directly proportional to the green chlorophyll in it, provided it matches in tint or hue the permanent standard. Then the colour of the extract can be expressed in *arbitrary units*, proportional to its chlorophyll content and proportional to the concentration of the permanent standard.[1]

[1] A permanent standard which is in use consists of a mixture of nickel sulphate and potassium chromate in dilute acid, the quantity containing $4{\cdot}6 \times 10^{-6}$ g. $NiSO_46H_2O$ and 25×10^{-6} g. K_2CrO_4 being taken as containing one arbitrary unit of yellowish green pigment (one *U.P.P.*). A green permanent standard has been matched with a mixture of pure chlorophyll *a* and *b* by Guthrie; when more yellow is added to this green standard, the quantity matching one *U.P.P.* is that which, without added yellow, matches a solution containing *c.* 0·003 mg. of chlorophylls *a* and *b*.

When the plankton is filtered from sea water and extracted with solvent, the solution is often an exact match in tint or hue as well as in depth of colour with a suitable dilution of the permanent yellow-green standard. At other times the residue after filtration contains detritus and pigmented animals from which yellow or brown pigments dissolve. Then all that can be done is to guess the dilution of the permanent standard which contains about the same degree of *green* colour. Such a guessed estimate may be very inexact. Attempts to overcome this limitation of an otherwise simple and rapid technique with simple apparatus have been unavailing. However, it should be possible with a sensitive spectrophotometer, because there is a marked absorption of light of wave-length 6550–6650 A. by chlorophyll *a*, while between 6200 and 6300 A. absorption is very much less (Fig. 3). Hence the difference in absorption by light of these two wave bands would give a direct measure of the chlorophyll content of an extract discoloured with yellow and brown pigments.

With extracts of net-caught plankton these difficulties of assessing the green colour rarely arise.

It was found by experiment that when trying to evaluate the green colour in an extract discoloured with yellow and brown pigments, by comparison with the standard solution, the quantity of green in the extract was usually overestimated. For this reason the values shown in Fig. 4 for phytoplankton retained by a membrane are maximal between June and September, during which period the extracts were discoloured. The probability of an overestimate during this period is indicated in Fig. 4 by a series of dots below the value actually estimated.

The *ratio of chlorophyll to organic matter* doubtless varies between algae of different species, and varies in any one species with the quantity of reserve material which has been laid down—diatoms are known to form droplets of free fatty acids in their cytoplasm, usually when growing slowly. Furthermore, when diatoms are grown in a dim light they appear browner and may contain a greater proportion of chlorophyll than when grown in a brighter light. However, if representative samples of phytoplankton are taken from whole water columns, and consist of many species, these differences in the ratio will tend to even out.

Data concerning this ratio of chlorophyll to organic matter, both direct and indirect, are sparse, but suffice to give a rough value of its magnitude.

On several occasions net hauls from bottom to surface in the sea off Plymouth have yielded catches consisting of diatoms with few zooplankton organisms, most of which could be separated from the catch. Analyses of these showed that diatoms containing one *U.P.P.* contained 0·00013 and 0·00010 mg. of phosphorus. Diatoms collected in the Gulf of Maine have been analysed by both Redfield and by Waksman; the mean value of their analyses show a ratio of C : N : P equal to 100 : 16 : 1·67. This indicates that their organic matter consisted of some 47% protein and 53% carbohydrates and lipoids, and con-

tained 0·75 % of phosphorus. Combining this value with that relating green colour to phosphorus content, the result indicated that diatoms containing one *U.P.P.* of green colour contained 0·0135–0·0175 mg. of dry organic matter. These deduced quantities of organic matter may be low, because the diatoms analysed for their C : N : P ratio were collected in the Gulf of Maine where the water is richer in phosphate than in the English Channel. Experiment has shown that diatoms grown in low concentrations of phosphate tend to contain less in proportion to their organic content.[1]

A culture of a brown chrysomonad flagellate was analysed by the writer. The quantity of this which contained one *U.P.P.* of green pigment was found to contain 0·0094 mg. of organic matter by loss on ignition. This value is probably too low, since the rather violent centrifuging necessary to concentrate the flagellates caused some to disrupt, discharging soluble organic matter into the water.

These estimates point to a mixed community, growing at all depths in the nutrient poor waters of the English Channel, containing about 0·016 mg. dry ash-free organic matter per unit of green colour or one *U.P.P.* This estimated ratio is no more than a rough approximation. It is unlikely to be less than half or more than double the true mean ratio. Rather many practical difficulties need to be overcome in order to improve this rough approximation.

A number of net catches consisting of diatoms, often with other plankton organisms, from the surface water of the Gulf of Maine have been examined by Riley (1941). From a regression equation it was found that diatoms containing one *U.P.P.* of green colour contained, on the average, 0·035 mg. of dry organic matter. This value may be higher than for a representative sample from all depths since the diatoms were collected from the surface layer. Various observations in the past, and a rough experiment by the writer, suggest that diatoms contain less pigment when grown in strong light than when grown in dim light, but further experiment is necessary to determine whether the light intensity affects the ratio of chlorophyll to organic matter in the diatoms.

[1] In addition to the classic observations by Ketchum on the marine diatom *Nitzschia closterium*, Redfield & Ketchum (1949) found that the fresh-water alga, *Chlorella pyrenoidosa*, grown in artificial light, accumulated much less phosphorus when grown in a phosphate-poor medium.

In culture rich in phosphate and nitrate, algae contained 2·69 % of their dry weight as phosphorus.

In culture deficient in phosphate and nitrate, algae contained 1 % of their dry weight as phosphorus.

In culture rich in nitrate, deficient in phosphate, algae contained 0·59 % of their dry weight as phosphorus.

In culture rich in phosphate, deficient in nitrate, algae contained 1·8 % of their dry weight as phosphorus.

It is of interest that the protein-carbohydrate-lipoid ratios in the organic matter of several fresh-water unicellular algae were very similar to that of a marine diatom grown under similar cultural conditions.

The Standing Crop of Phytoplankton

During 1949 a position 5 miles seaward from Plymouth, having 50 m. depth of water, was sampled at intervals. Hauls with a net of fine bolting silk, having, when wet, meshes with pores of $41 \times 52\,\mu$, were made through the whole water column from surface to bottom; the quantity of water filtered being registered by a meter in the mouth of the net. The catches were extracted with solvent and the green colour estimated. The result is shown in Fig. 4. It shows similar seasonal variations but lesser quantities than found in a series of observations made in exactly the same manner throughout 1933 and 1934.

At the same time, equal quantities of water, collected from 5, 15, 25, 35 and 45 m. depth, were mixed to give a *composite sample* representative of the whole water column. Two-litre portions of the composite samples were filtered through a small disk of Whatman no. 2 filter-paper under a head of 2–3 cm. of water. The residue was extracted with solvent and the depth of green colour determined. From observations in Long Island Sound, Riley had concluded that this filter-paper held back 90% or more of the phytoplankton organisms, little more being held back by a membrane filter. On and after 26 April filtration through a Gradocol membrane, average pore diameter $0{\cdot}9\,\mu$, was adopted. Extracts of the phytoplankton collected on filter-paper contained less green than extracts collected on the membrane.

Composite sample collected	Green colour, expressed in *U.P.P.* per cubic metre of water: By filtration through paper	By filtration through membrane
26 April	7,500	12,000
7 May	6,000	11,000

On both occasions the water contained many small flagellates. The tint or hue of the extract was similar to that of the nickel standard.

At the end of May a notable quantity of organic detritus had accumulated in the water; and from then until August the extracts were seriously discoloured with yellow-brown pigments.

Provided the depth of water exceeds the depth of the photosynthetic zone, it is of interest to compare the standing crop of phytoplankton below unit area of the sea at different positions. The mean value of a number of observations made in the Gulf of Maine on seven occasions are plotted in Fig. 5. Water samples had been filtered through Whatman no. 2 filter-paper and the green pigment extracted from the residues was estimated. It is seen that in that sea-area, where the nutrient-salt content is over three times greater than during recent years in the English Channel, the chlorophyll in the plants below a square metre is considerably greater than in the water off Plymouth.

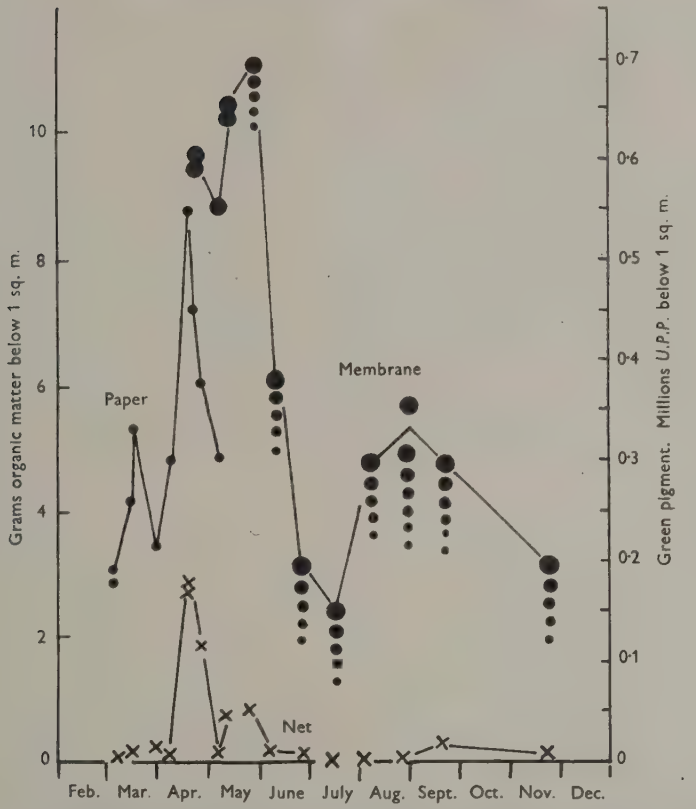

Fig. 4. The quantity of green pigment and the (calculated) quantity of organic matter in the phytoplankton at a position 5 miles seaward from Plymouth during 1949.

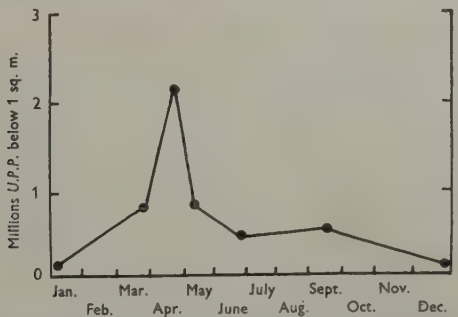

Fig. 5. Phytoplankton population on George's Bank, Gulf of Maine, in terms of units of plant pigment below a square metre. (After Riley, 1946.)

The standing crop in that deeper, and nutrient-rich, sea-area is about five times greater than the standing crop in the Plymouth area during 1949—a year when the water was notably poor in nutrients.

The Annual Production of Phytoplankton

In the Plymouth sea-area there is evidence that the majority of the larger phytoplankton organisms are eaten by zooplankton organisms. These discharge great numbers of green faecal pellets into the water when plant life is abundant. The pellets, the organic detritus resulting from them, and some few plants provide the vegetable food of the filter-feeding bottom-living animals. Deposition of organic detritus or dead plants on the floor of the open sea in this area appears to be negligible in quantity. Over the whole year, or over the first 6 months of the year, the quantity of phytoplankton produced approximates to the quantity grazed by zooplankton in the water column. Yet only a portion of the plants which are eaten in the water column are fully digested.

The standing crop of plants at any moment is the resultant balance between the rate at which they have been produced and the rate at which they have been eaten.

The rate of production is influenced by an array of factors, in addition to the number of growing plants in the photosynthetic zone. As the year advances the decreasing concentration of nutrient salts reduces the rate of multiplication progressively, until the rate of their replenishment in the water of the photosynthetic layer balances the rate at which they are being utilized. This rate of replenishment exercises a major control over the monthly production during the summer. If the nutrients were not being continuously replenished plant growth would not only be slowed but soon stopped through lack of nitrogen and phosphorus in available forms.

The reduction in quantity of nutrient salts in the water column between winter and summer is readily determined. This quantity, plus that which has been excreted by the animals or otherwise reformed, has meanwhile been built up into plant tissue.

Between February and June in 1948 and again in 1949, the decrease in phosphate below a square metre at a position 20 miles off-shore from Plymouth amounted to 0·49 g. P. During this interval, in both years, there is evidence of water movement having taken place, the richer water present in January having been replaced by water containing less total phosphorus (Armstrong & Harvey, 1950). A more probable value for the decrease in phosphate since January below a square metre in the water actually present in June is 0·40 g. P below a square metre.

If these quantities were built up into phytoplankton some 53–65 g. of dry ash-free vegetable tissue would result. Meanwhile, during the 5 months, phosphate was being excreted and regenerated in the water and this also utilized by plants. The 53–65 g. of vegetable tissue is an estimate of the

minimum quantity of plant tissue produced; in all probability it was greatly exceeded.[1]

Minimal estimates of production during the first half of the year have been made by Atkins (1928) and by Cooper (1933) in previous years, from the decrease in phosphate, in nitrate, in carbon dioxide and from the increase in dissolved oxygen. The values range from 85 to 190 g. of organic matter in the 6 months.

During the second half of the year the standing crop is less. In addition, the low concentration of nutrients slows the plants' growth rate. It is not until after mid-September that any material increase in nutrients occurs in the upper layers. By this time the quantity of light is half that in summer and is falling rapidly (Fig. 6). Thus, there is almost certainly less production during the second half of the year.

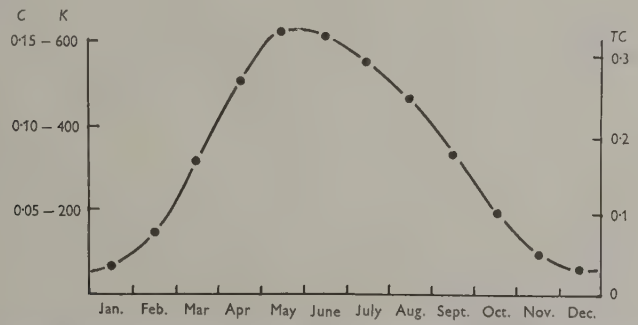

Fig. 6. Average illumination at Plymouth for the years 1930–37. *K*, kilolux hours per day; *C*, gram calories per cm.^{2} per min., both for light within the range 380–720 mμ wavelength. *TC*, deduced total solar radiation, which includes infra-red, in g./cal. per cm.^{2} per min. (From data by Atkins, 1938.)

These various considerations and minimal half-year estimates provide reason to expect that the total production throughout the whole of 1949 is unlikely to have fallen short of 120–200 g. of organic matter below a square metre (an average of 0·4–0·55 g. daily), and may have been considerably more.

It is of interest to compare this assessment of the annual production of organic matter by plants in this nutrient-poor area with an assessment based on entirely different premises in another sea area.

[1] Observations made in this area and in Loch Striven suggest that during March the diatom population in the whole water column divides on the average once in 36–38 hr., with the production of 50–70 % of its own weight of organic matter daily. From Fig. 6 it is seen that the incident light in March is roughly the average of that for the period January to June; the temperature is rather less than the average over this period. On the other hand, during April and May the concentration of nutrients in the upper layers falls rapidly. Hence for the first 5 months of the year there is suggested a daily production of rather less than 50 % of the biomass of the standing crop. If a value of 30 % daily is assumed, and the mean biomass over the first 5 months is 5–6 g. organic matter below a square metre (Fig. 4), then the production during this period amounts to 250–300 g.

A very rough assessment of the whole annual production of phytoplankton in the Gulf of Maine has been made by Riley in the following way. Transparent and black bottles were filled with the water, kept at sea temperature in a barrel of water for one or more days and the resulting difference in oxygen content of the light and dark bottles determined. This difference gives a direct measure of the gross production by the plants, that is the quantity of carbon synthesized, and takes no account of their losses meanwhile by respiration. The latter were calculated from the estimated quantity of plant life in the water and subtracted from gross production. From the depth of the photosynthetic zone, month by month, in the area and the relative light intensities, the carbon synthesized below a square metre was roughly estimated. In the following table, the quantity of organic matter has been substituted for the quantity of carbon, to make these readily comparable with the quantities already considered in this essay. Analyses of diatoms had shown that 2·24 g. of organic matter contain 1 g. of carbon:

	Organic matter produced below 1 m.² in g. per day
January	−0·112
March	+0·425
April	2·1
May	1·2
June	1·4
September	0·31

This indicates the production of some 160 g. organic matter below 1 m.² during the first 6 months of the year, and 270 g. during the whole year, an average of 0·8 g. daily. This includes the organic matter produced from nutrients which may have been used, excreted and used again.

Factors Affecting the Annual Production of Vegetation

Having considered the sequence of plant life and the quantities involved, it is of interest to consider the major factors which determine the annual production of vegetable tissue.

The production taking place at any moment is the quantity of the standing crop multiplied by its *mean* rate of multiplication. Only those cells can grow which lie within the photosynthetic zone.

The quantity or *size of the standing crop* varies as it is either reduced by being eaten or is allowed to increase. Increase occurs when production exceeds losses due to grazing and losses due to respiration of those phytoplankton cells which are carried or sink below the compensation level, where they dwindle, being no longer able to make good their respiratory losses by photosynthesis. Observations on respiration by phytoplankton organisms indicate that at a sea temperature of 10° C., they lose some 4% of their organic matter daily when kept in the dark.

While phytoplankton cells are multiplying there appears to be little tendency

for them to sink, but as growth slows down owing to lack of nutrients, or light, or other ill-defined causes, the cells tend to lose buoyancy. Besides this, turbulence set up by rough weather, particularly between October and May, when a thermocline is absent, also carries cells to below the compensation level, thereby depleting the growing stock.

These losses may be small compared with those due to the continuous grazing by zooplankton, and, in shallow waters particularly, by filter-feeding bottom-living animals. Otherwise there would be a great accumulation of sinking organisms in the water column below the compensation level.

The *rate of multiplication* of the standing crop, or rather that portion of it within the photosynthetic zone, is most notably dependent upon the amount of light falling day by day upon the sea, and upon the concentration of nutrients. In some areas the availability of other microconstituents in the water probably affects the rate of multiplication.

The species composition of the standing crop will also influence its growth rate as a whole, since the different species composing the population have different light requirements for optimum growth rate, and these rates vary between different species. Smaller cells tend to grow faster.

The depth of the photosynthetic zone at any moment varies with the intensity of light falling on the sea, and in consequence so does that proportion of the standing crop which is making growth. Although the proportion of the light falling on the sea from month to month is much the same each year, the total quantity during any year varies materially. Thus from 1930 to 1937, the quantity of daylight falling on this laboratory varied between a daily mean of 307 kilolux hours in 1937 and 412 in 1930 (Atkins, 1938). Hence in a particular sea-area, changes in the quantity of incident light from year to year are likely to affect plant production.

The concentration of nutrients at any moment in the water in the photosynthetic zone, where it can be used by the plants, is the accumulated excess due to greater replacement than utilization. Replacement takes place by excretion from animals, by regeneration from dissolved organic nitrogen and phosphorus and by nutrients rising into the photosynthetic zone from below due to vertical mixing by turbulence. As far as we know, from experiments with one species only, the concentration of nutrient salts in the English Channel has, for several years, always been less than optimum, and in summer always acts as a powerful brake on the rate of growth.

A mathematical analysis of observations in the Gulf of Maine suggests that the availability of nitrogen and of phosphorus alternate in exerting the greater depressant effect upon growth rate during summer months.

It is helpful to consider the production of vegetation under simplified, hypothetical conditions, where the depth of water is similar to that of the photosynthetic layer. This implies little change in light intensity from season to season, a condition which may be approached in tropical areas. Plant pro-

duction throughout the year would be maximal if the standing crop kept the concentration of nutrients at such a low level that the daily increase in plant life, and never more, was grazed by zooplankton and the plants utilized the nutrients as quickly as they were being reformed. Thereby the dissolved organic nitrogen and phosphorus would be kept at a maximum, and the rate of replacement of nutrients both by regeneration from it, and by excretion from animals, at a maximum also.

In waters of depths greater than the photosynthetic zone replacements of nutrients, or their immediate precursors, by turbulent diffusion from below, plays an increasingly important part. Zooplankton rise by night to feed in the upper layers, then fall by day and excrete below the zone some of the combined nitrogen and phosphorus which they have collected. There is thus a continuous drain from the upper layers to the water below. Turbulence is the means by which this drain is compensated. Our observation of phosphorus compounds in the water column indicates that this drain downwards becomes pronounced only after the thermocline has formed. Throughout the period of spring diatom maximum, turbulence is sufficient to offset it. In this way turbulence contributes to production, while at the same time reducing production by carrying plant cells downwards.

Present knowledge shows that the production of plant tissue in the sea from day to day depends upon:

(i) The rate of regeneration of nutrients from dissolved organic compounds, particularly within the photosynthetic zone.

(ii) The quantity of nutrients rising by turbulent motion from below.

On (i) and (ii) depends the continuance of growth.

(iii) The population density of zooplankton eating the stock of growing plants.

(iv) The rate of loss of growing cells due to sinking below the zone. This is largely occasioned by turbulence, particularly in winter.

(v) The mean depth of the photosynthetic zone throughout each 24 hr. This varies with the quantity of light falling daily on the surface of the sea (Fig. 6) and with the transparency of the water.

On (iii), (iv) and (v) depends the magnitude of the growing stock, or quantity of photosynthesizing phytoplankton.

(vi) The considerable effect of temperature on the respiration rate of the plants, which tends to be offset by its effect upon the rate of regeneration of nutrients and upon the rate of photosynthesis.

(vii) The concentration of nutrients in the water within the photosynthetic zone. These consist of nitrogen in the form of ammonia, nitrate, nitrite and some amino-acids, and of phosphorus in the form of phosphate and probably of some organic phosphorus compounds.

(viii) The concentration of some other constituents of sea water (*vide infra*).

On (v), (vi), (vii) and perhaps (viii) depends the growth rate of the growing stock of plants.

In nature all these eight factors vary continuously, and most are interdependent upon one another.

Riley's analyses of survey data in several areas have indicated the relative influence of some of these factors and of how their influences change with the seasons. Before this valuable mathematical tool can be used in this area, a reasonably accurate technique of estimating the standing crop of phytoplankton needs to be evolved. However, a consideration of the rather complex and changing picture, which these eight factors presents, leads to a conclusion relevant to this thesis.

In comparing conditions from year to year in the area, small differences in the overall conditions of light, turbulence and temperature are likely to be subordinated to the big differences which may occur in the totals of all forms of combined nitrogen and phosphorus in the water. In the early 1920's there was twice as much as in recent years: one would expect that this difference alone doubled the regeneration and supply of nutrients to the growing plants, thereby doubling the production of vegetation except for a short period in the winter.

The possibility that microconstituents, other than nutrients, in the water may affect the growth rate of phytoplankton in nature is indicated by experiments *in vitro*. These have shown that very minute additions of salts, of iron, of manganese, of other elements, and of several organic compounds, increase the division rate of many species of plankton algae growing in sea water enriched with nutrient salts. Hence it is possible that varying concentration of some of these substances in the sea may affect the production of phytoplankton. Observations by Hart in the South Atlantic actually indicate that, in these nutrient-rich waters, the supply of some constituent derived from land drainage allows the much heavier development of plant life which occurs in some areas than in others. There are numerous observations which show that the multiplication rates of *particular* species of phytoplankton differ in different sea waters into which they have been introduced, due to microconstituents other than nutrients and iron. It is not known what constituent or constituents may be lacking, nor indeed whether there may be inhibitory organic compounds in the water. Somewhat indefinite evidence of the presence of inhibitors in some waters is provided by experiments by Allen & Nelson (1910) which showed better growth of diatoms after nutrient-enriched waters had been treated with hydrogen peroxide, chlorine or charcoal.

The list of substances which promote growth of marine plants is increasing. Concerning one of the more obvious essentials for growth the following is of interest. The quantity of manganese in an available form in the waters off Plymouth has been shown by experiment to be insufficient for a luxuriant growth of several species of autotrophic flagellates. Samples of water from an area in the Irish Sea, where flagellates are noticeably abundant, contained more than twice the concentration of available manganese found in this area. The inference

that in nature varying concentrations of this element influence the growth rate of these species seems justified.

In temperate seas, where low concentration of nutrients limits the annual production, a greater rate of multiplication of the plants would correspondingly increase production before and after the duration of the thermocline, and during these periods would allow the plants to keep down the concentration of nutrients to an even lower level. By so doing the dissolved organic nitrogen and phosphorus in the water column are increased, and the rate at which the phosphate and ammonia are released is increased also. In this way, the effect of a greater multiplication rate would be similar to the effect of more intense illumination in early spring and autumn, and would increase the turnover of nitrogen and phosphorus compounds.

The Zooplankton Community

The wide variety of species in the zooplankton community differ greatly both in size and in their content of water. Moreover, there are considerable differences in the proportion of water in zooplankton from different areas, which are ascribed to differences in quantity of stored lipoids, this again being dependent upon the supply of phytoplankton food. It is, in consequence, desirable to express the quantity of such a mixed community in some one form. The content of dry organic matter is suitable and provides a measure of the value as food for other animals.

The population density of zooplankton organisms, expressed either as number or weight per *unit volume*, provides a measure of their *availability* as food for other animals. The quantity of zooplankton below a *unit area* of the sea is the *quantity maintained* by the vegetation produced in the water below that unit area. Moreover, the quantity below a square metre of the sea, expressed as weight, allows comparison to be made with observations made elsewhere. Comparable observations have been made, notably off the American Coast and in the Northern Sargasso, where quantitative catches have been dried and ashed, the loss on ignition providing a direct estimate of the organic matter.

The two ecological groups of which the zooplankton is composed—the plant-eating and the wholly predatory organisms—merge into one another; there is no sharp line of distinction between them. From limitations imposed by their size, the smaller organisms are likely to be herbivores. Many of those of medium size are omnivores, and the remainder, forming a small but very varying part of the community, are predominantly carnivores. Many of the latter are of relatively large size—ctenophores, medusae, arrow worms, *Tomopteris*, and the early planktonic stages of young fish. An exceptional group are the Salps which, although of relatively large size, are predominantly herbivorous. The effect upon the community of these purely predatory organisms is enhanced by the depredations made by pelagic fish, and by

omnivorous filter-feeding, bottom-living, organisms, more particularly in shallow water.

Almost always the bulk of the zooplankton is composed of the plant-eating group, and of these the bulk consists of juvenile copepods and their nauplii, with a variable, usually small, proportion of the larvae of bottom-living organisms. These latter spend a limited time, between a week and 2 months, forming the *temporary plankton*, whereas the life span of the copepods, from egg to adult, varies around 6 weeks, with the exception of the brood which lives over the winter months.

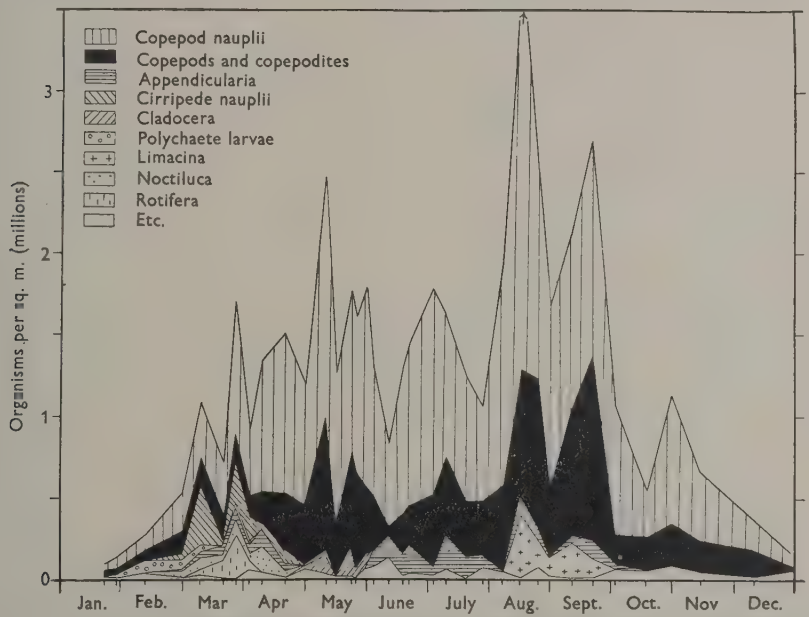

Fig. 7. Number of zooplankton organisms in millions caught in net, below a square metre in the sea off Plymouth, with a depth of 50 m., during 1934. (Harvey, Cooper, Lebour & Russell, 1935.)

Twice a month throughout 1934 several vertical hauls were made with a fine silk net at a position 4 miles off-shore from Plymouth, in 50 m. of water. The quantity of water filtered was registered by a meter, and the organisms in an aliquot of the combined catches were counted. The composition of the catch from the water at this position on the various dates is shown in Fig. 7.

The phosphorus content of the animals in a second aliquot of the catch was determined. From their phosphorus content an approximate value of their organic matter can be derived. Analyses of mixed communities, mostly copepods, show them to contain about 83% of water and 0·2% of phosphorus.

Analyses of zooplankton quoted by Fleming give a C : N : P ratio of 40 : 7·4 : 1 which implies 87 times more dry, ash-free, organic matter than phosphorus.

The values shown on the right of Fig. 8 are derived in this way. After attaining a maximum in early May, the summer population below a square metre fluctuates around a density containing some 2 g. of dry ash-free organic matter, with a significant increase in September. This autumn increase appears to be of frequent occurrence in other areas, and in some to occur before any autumn increase in phytoplankton would be expected, and before the summer population of predatory zooplankton is likely to have died away.

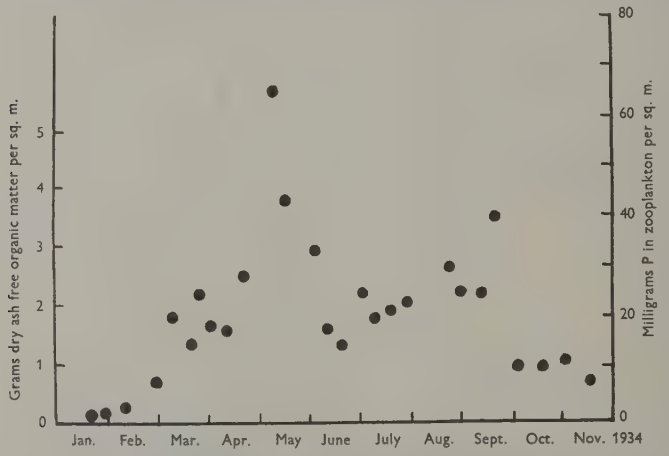

Fig. 8. Organic matter and phosphorus in zooplankton below a square metre, in 50 m. depth, off Plymouth. (Data from Harvey *et al.* 1935.)

During the summer of 1949, a considerable number of vertical hauls were made in the area using larger nets with meters to register the quantity of water filtered. The primary aim was to determine the patchiness of the distribution of the plankton. So far, it appears that the values shown in Figs. 7 and 8 are a reasonable rough approximation to the mean population density over the area. The catches in 1949 ranged from 1 to 1·7 g. dry weight (0·85–1·45 g. organic matter) below a square metre. These are significantly less than found in 1934, when the water contained more nutrient salts in solution at the beginning and at the end of the year.

In June 1947, a series of hauls were made at intervals throughout 24 hr. at two positions in the English Channel. These show the variation between one catch and another made in substantially the same body of water, and also indicate the proportion of the biomass which was present as macroplankton caught in the larger net. Vertical hauls between surface and bottom were made with a silk net having a mesh with openings 0·2 × 0·2 mm., and oblique hauls were made between 35 m. and surface with

a stramin net having meshes 1 × 1 mm. With the latter, the catches varied considerably in quantity, partly due to diurnal migration; hence, for purposes of comparison, the catches made at midnight, when the largest number of organisms have migrated into the upper layers, were chosen.

The composition of the catches shown in wet weight per cubic metre of water filtered is given in Tables I–III.

TABLE I. CATCHES MADE WITH SILK NET 20 MILES SEAWARD FROM PLYMOUTH. ALSO WITH 2 M. STRAMIN RING TRAWL, HAVING 1 MM. MESH IN OBLIQUE HAUL BETWEEN *C.* 35 M. AND SURFACE. 9 AND 10 JUNE 1947.

	Wet weight in milligrams per cubic metre of water filtered			
	Copepods, mysids, euphausians, and decapod larvae	Medusae	*Sagitta*	Young fish
Silk net				
Afternoon	105	3	—	—
Dusk	85	—	—	—
Midnight	130	2	—	—
Dawn	145	—	—	—
Midday	195	—	—	—
Afternoon	115	2	—	1
Mean wet weight	*130*	*2·5*	—	*0·02*
Stramin net				
Midnight	3·6	—	0·7	0·23

TABLE II. CATCHES MADE WITH SILK NET AND WITH 2 M. STRAMIN RING TRAWL AT 49° 22′ N., 6° 12′ W., BEING 30 MILES SOUTH OF THE SCILLY ISLES. 28 JUNE 1947.

	Wet weight in milligrams per cubic metre of water filtered			
	Copepods, mysids, euphausians, and decapod larvae	Medusae	*Sagitta*	Young fish
Silk net				
Morning	172	35	19	0·2
Midday	201	—	48	—
Afternoon	165	18	26	—
Dusk	174	57	8	11
Midnight	140	—	0·5	—
Mean wet weight	*170*	*22*	*20*	*2*
Stramin net				
Midnight	5·6	36	5·5	1·1

Subsequent analyses of the catches made with the silk net allow mean values of the population density below unit area to be calculated.

TABLE III. ORGANIC MATTER IN ZOOPLANKTON BELOW 1 M.^{2} CAUGHT IN 0·2 × 0·2 MM. MESH NET (G.).

20 miles south of Plymouth	1·6
30 miles south of Scilly Isles	3·5

The estimates made in 1934 and 1949 indicate that the water off Plymouth maintained an average of some 2 g. of organic matter in the form of zooplankton

below a square metre, after the population peak in April 1934 until October, and a smaller quantity in 1949.

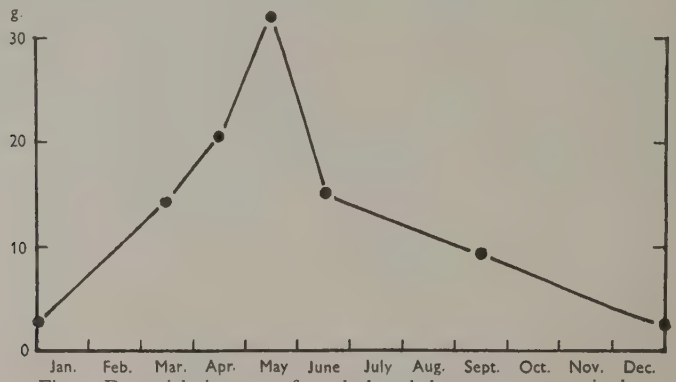

Fig. 9. Dry weight in grams of zooplankton below a square metre in the Gulf of Maine. (After Riley & Bumpus, 1946.)

It is of interest to compare these quantities with those found in other areas. The nutrient-rich waters of the Gulf of Maine, after the peak population in April or May, maintain some 12 g. dry weight of zooplankton, containing about 10 g. of organic matter, below a square metre. The waters of the Northern Sargasso between July and September were found to maintain zooplankton containing 1·4 g. organic matter. This quantity is rather less than that maintained off Plymouth in 1934; the standing crop of phytoplankton also appears to be less, or at least to contain less chlorophyll.

Food of the Zooplankton

In general, the metabolic rate of small organisms is greater than that of larger ones; equal weights of vegetation will support the life of much less bacterial or small zooplankton tissue than, for instance, lamellibranch tissue.

Small animals not only need more food to make up for their greater metabolic rate than do larger animals, but, in general, weight for weight, they collect and partially digest a much greater quantity. For instance, the larvae of large bivalves, weight for weight, filter very much more water than the adults. They are stated, weight for weight, to digest and oxidize to carbon dioxide a hundred times more food.

In addition to requiring more food to make good their greater respiratory losses, the smaller animals are likely to be more wasteful of the primary vegetable food supply. When a plant is eaten, broken and only partly digested, a quantity of protein and carbohydrate dissolves and escapes into the water. Some of this is used by a sparse flora of bacteria, and possibly, a little by other micro-organisms. The solution is so dilute that the dissolved organic matter

is not at all readily available. Much of it is surely oxidized by oxygen in the water without being built into the bodies of bacteria. This is entirely lost to the food cycle. For this reason, the feeding habits of organisms in the zooplankton community is of interest.

Many wholly carnivorous species contain much more water than the herbivorous crustaceans—arrow-worms twice as much, ctenophores or medusae ten to twenty times as much—hence, although they may appear bulky, their organic content is usually small compared with that of the omnivores and herbivores forming the remainder of the community. The quantity of the latter which the carnivores succeed in catching and destroying is unknown, but on occasions their depredations appear to be great. During July 1949, an area was encountered in the mouth of the Channel, in 6° W., with a macroplankton fauna very considerable in comparison with that in the water off Plymouth, and consisting largely of medusae and the planktonic worm *Tomopteris*. Catches with a fine silk net consisted mostly of these worms, while copepods and other crustaceans were almost entirely absent; the quantity of these latter below a square metre was only a small fraction of that in the water off Plymouth. These facts indicate that *Tomopteris* is a voracious predator, and had succeeded in eating almost all the omnivores and herbivores. Of the other carnivores, the voracity of ctenophores is well known. Bigelow has noted that the smaller plankton animals are locally exterminated in the centres of abundance of *Pleurobrachia*, which is commonly found packed with copepods or euphausians as well as with larval fish.

The copepods, during their earlier stages, are probably from their very size mostly herbivorous, feeding upon phytoplankton. In their later stages many are omnivorous, eating whatever organisms they are able to catch. Some species, as *Temora* and *Centropages*, are notably voracious, and their stomach contents have been seen to consist of other crustaceans and of diatoms. If a *Calanus* is placed in a dense population of diatoms, it can be seen to extrude green faecal pellets at 20 min. intervals. For greed, voracity and wasteful feeding, many planktonic crustacea are unmatched.

During 1933 and 1934, when frequent observations of the population of the phytoplankton large enough to be caught in a net were made, great numbers of such green faecal pellets were found in the water at the time and immediately after the population of the larger diatoms had risen to high values. That this heavy grazing is not limited to the larger plants is indicated by an analysis of observations made in the Gulf of Maine, although it is perhaps the sudden changes in the population density of the larger plants which show the effect of grazing most clearly.

Although the biomass, or quantity of organic matter in the form of zooplankton does not change greatly during the summer, growth is proceeding all the time and providing a daily quota of food for other organisms.

There exist observations on the life history of *Calanus finmarchicus* which

allow a rough estimate of the rate of increase in the biomass of individuals of this species during the summer months. It is reasonable to consider this species as rather typical of other copepods, and it is copepods which constitute the bulk of the zooplankton population. A period of some 50 days between egg and sexually mature adult appears usual during the summer, a very much longer period during the winter. The diameter of the egg of *Calanus* is recorded by Gibbons as 0·172 mm., indicating a wet weight of 0·005 mg. The wet weight of sexually mature individuals appearing in the Plymouth waters in summer is recorded as around 0·8 mg. Hence in the 50 days there has been a 180-fold increase in wet weight. In order to proceed with a calculation, an assumption is made that the percentage of dry organic matter in the egg is roughly the same as in the adult. A further assumption is made that the daily percentage increase in weight remains constant during the whole period of 50 days; in actuality there is likely to be a short lag period before logarithmic growth starts and a slowing towards the end of the period. From the equation of geometrical increase, $Q_t = Q_0 \epsilon^{kt}$, t being 50 days, the daily increase is 10% of the weight.

There is an independent method of arriving at a rough estimate of this daily percentage increase. During the 50 days between egg and adult, some sixty young are reduced in numbers to two, the two necessary to maintain the population. Meanwhile, the creatures are being eaten steadily. If they are eaten at a rate proportional to their population density, the fall in numbers from sixty to two in 50 days indicates that 7% are eaten daily. The two estimates (of the daily percentage increase in weight, and of the percentage eaten daily by other animals) are in reasonable agreement.

Concerning the food required by the zooplankton, it is helpful to distinguish between the quantity which is assimilated, and which is either burnt to carbon dioxide in the respiratory processes or is built up into the growing animal, and the quantity which is eaten in excess of that assimilated.

Experimental evidence provides a measure of how much of their body substance is required to be made good in order to compensate for the daily loss by indicated respiration.

Computations, shown in the previous paragraphs, indicate how much is built up daily into the growing animals—from 7 to 10% of their own weight.

A great variety of animals have been kept in closed containers and the oxygen used by them estimated after a short interval. They appear neither to have been starved nor heavily fed, nor to have been entirely inactive. It seems permissible to assume that the respiration rates found experimentally averaged those of animals growing normally, and, after adjustment for temperature, indicated their average rates when living in the sea.

Experiments with both *C. finmarchicus* and with a mixed community of crustacean plankton indicate that the animals 'burn' 4% of the carbon in their

tissues daily, at our summer sea temperature. From descriptions of the experiments the animals had not been starved. From this it is concluded that, of the food which they normally collect and pass through their guts, a quantity of vegetable tissue equal to about 4% of the animal's tissue is assimilated daily and broken down to carbon dioxide. In addition, a quantity equal to 7–10% of the animal's tissue is built up into the growing animal. It is unknown whether these lowly animals need the whole range of amino-acids required by mammals, and it is unknown whether phytoplankton protein is deficient in any one or more amino-acids required by the zooplankton. Thus it is possible that the animals need to digest and absorb more vegetable tissue than the sum of the quantities burnt in respiration and built into their own growing bodies.

For simplicity and in order to arrive at a rough calculation it is permissible to treat the whole zooplankton community as herbivores, and the plants as not being deficient in any necessary amino-acid.

It then follows that the population below a square metre of the sea, containing on the average 1·5 g. of organic matter will require to *assimilate* daily: 4% or 0·06 g. of vegetable organic matter to make good respiratory loss; 7–10% or 0·15 g. to build up into new tissue and provide the daily quota which is used by other animals.

Thus, in this single step in the food chain—vegetable tissue to small quick-growing animals—about 30% of the vegetable tissue assimilated is lost as carbon dioxide and 70% converted to animal tissue.

The zooplankton animals collect and eat more food than they assimilate. Judging by the habits and great voracity of many zooplankton organisms, and by the number of their faecal pellets to be found still coloured green in the sea, they succeed in collecting much more when phytoplankton is abundant.

Since plant life is sparse during periods in the summer, it is of interest to consider how the zooplankton succeed in collecting their ration.

Experiments by different observers with the large planktonic copepod, *Calanus finmarchicus*, have shown that it can filter very small diatoms from 4 to 5 c.c. of water daily.

This suggests that if the whole summer population were to consist of adult *Calanus*, the animals below a square metre could filter the very small plants from only about 100 l. of water daily. The weight of plant tissue in this quantity of water is negligible.

Experiment has shown that *Calanus* can catch larger diatoms very much more efficiently than they can filter very small ones. Kept in a suspension of medium-sized diatoms, in an hour each caught the number originally present in 3 c.c. of water. Kept in a suspension of large-sized diatoms each caught in an hour the number originally present in 8 c.c. of water. It is of course possible that in these experiments, where the diatom population was dense compared with that in the sea, the *Calanus* did not exert their catching power to its fullest extent.

The results of these experiments suggest that if the summer population below a square metre consisted of late-stage *Calanus*, it might catch the larger diatoms in 2000–3000 litres of water daily. Then, for the zooplankton to live entirely on plants, a cubic metre of the sea would need to contain 100 mg. of organic matter in plants large enough to be caught in a net.

A population density of plants such as this is of rare occurrence during the summer. We do not know how diatoms are distributed with depth in the waters off Plymouth, but, judging from other areas, they are most concentrated in the upper 30 m. Taking this into consideration, our records indicate that this population density of netable plant tissue occurred only on five occasions out of twenty-eight during the summers of 1934 and 1935.

During these years the average size of the organisms forming the zooplankton community was only a fraction of that of late-stage *Calanus*. The smaller animals are, weight for weight, probably more efficient in collecting food than the larger organisms, particularly in filtering the smallest plants.

It appears that the filter-feeding mechanism of the larger zooplankton organisms is not so highly developed that they can obtain much of their food by this method. Indeed experiment with *Hemimysis* has indicated that it could collect no more very small diatoms than an adult *Calanus*, which is about one-eighth of its size.

The zooplankton doubtless obtains some food by eating planktonic larvae, eggs, and sperm cells discharged into the water by lamellibranchs and other bottom-living animals. As each one spawns it discharges a considerable fraction of its own weight into the water. However, the daily supply from this source is not likely to contain on an average more than 0·05 g. of organic matter per square metre per day over the summer months, unless the quantity of bottom-living animals has been grossly underestimated.

During the periods of diatom scarcity the copepods' guts are often seen to contain pale brown matter, similar to the once-eaten plants which form most of the organic detritus then in the water. This detritus remains suspended in the water column for a considerable time, kept stirred by tidal streaming and wave action. It seems likely that this detritus, consisting of once-eaten plants, plays a considerable part in the food chain.

Fluctuations in Population Density

Quite considerable fluctuation may occur from year to year in the average population of zooplankton maintained by the water occupying particular areas of the sea. Observations with the Hardy plankton recorder show this in various areas of the North Sea. It is pertinent to consider likely causes of these fluctuations.

Almost everywhere in the seas there is renewal of the water taking place from time to time, in some places frequently. Waters passing through any area are likely to have different biological histories in their immediate past, and in

consequence to have different contents of nutrients for plant growth or to have different rates at which these are being regenerated from dissolved organic nitrogen and phosphorus compounds. This in itself will bring about fluctuations from year to year in the plant food for the zooplankton. More zooplankton may be expected to be maintained where there is more phytoplankton over a sufficient period of time for temporary changes in the populations to be ironed out. Comparison of one area with another has long indicated this in a general way, and the more recent quantitative observations by Riley *et al.* all bear out this belief. Moreover, from observation of the changing populations of diatoms and copepods in a Scottish Loch, where the water is subject to little interchange with other water masses, Dr Marshall (1949) concludes that 'on the whole it does seem that the presence of diatoms increases the production of eggs and nauplii and helps the development of the younger stages' from time to time during the course of the year. Experiment indicates a similar relationship, since by enriching a tank of sea water with nutrient salts Clarke & Gross (unpublished) have induced a population density of copepods to develop in the water, amounting to several thousands per litre—a remarkable population density when compared with the 50 per litre found in the sea.

Another cause of fluctuations may be due to the copepod population being preyed upon to a different degree from year to year by migratory pelagic fish, or even due to the proportion of carnivorous zooplankton changing materially and for long enough to upset the balance seriously.

Of these two causes of fluctuations in a sea-area, supply of vegetable food appears to predominate. There may well be other circumstances which change from year to year and which play a part in controlling the copepod population, although these are not obvious. A rather remarkable distribution has been observed in the southern North Sea (Rae & Fraser, 1941). In 1920 and 1921 there occurred in January and December a considerable zooplankton population off the coast of East Anglia, and in the winter of 1933 off the Dutch coast. This has been attributed to heaping caused by the prevalent wind drift of the upper water layers, and presupposes that during the long winter nights the organisms spend most of the 24 hr. near the surface and a lesser period in the compensation current flowing in the deeper layers. These observations, and the inferences to be drawn from them, suggest a mechanism which may play an important part in regulating the distribution of zooplankton in some coastal areas.

When the population densities of two different areas are compared, another factor, and a potent factor, needs consideration. Vertical turbulence, and its effect on the production of plants, is unlikely to be the same. By renewing the nutrient salts in the photosynthetic zone in one area more rapidly than in another, plants are enabled to grow more rapidly so that a similar standing crop of plants can provide a greater daily supply of food for copepods. Yet, in

spite of this, and of differences in the depth of the photosynthetic zone, and of differences in temperature, the population per unit area of zooplankton does seem to follow roughly that of the phytoplankton in very different sea areas. Our present knowledge points to the average standing crop of plants usually predominating over other causes in controlling the average population density of zooplankton, provided the sea-areas compared with one another are of considerable extent. Within such areas there are liable to be extensive patches where diatoms abound, as in the southern North Sea, in which the zooplankton is less abundant than around the edges of the patches. These patches presumably arise and persist because the intensity of grazing within them is less than in the surrounding waters.

Pelagic Fish

It is possible to make a rough estimate of the quantity of pelagic fish, mostly herring, in the North Sea, extending over some 170,000 square miles. During the 1930's roughly one million tons of herring were landed each year. Of the various year classes caught during any one year, about one-half the quantity is caught during the following year—the annual mortality of adult fish is 50% from all causes. About three-fifths of this mortality is ascribed to fishing, which is to say that 30% of all adult fish were caught annually. Hence the quantity of adult fish in the area is some three million tons. To this quantity there needs to be added the smaller fish not large enough to be enmeshed in the herring nets, that is, fish up to and including many 3-year-olds. It is only possible to guess that their weight may be a third or even more than that of the older fish.

If these two assumptions are accepted: (i) that fishing accounts for three-fifths of the natural mortality of the older fish, and (ii) that the younger fish, not enmeshed in the nets, aggregate one-third of the larger fish, then the total population amounts to four million tons.

The population would then, if evenly distributed, comprise 1·8 g. of dry organic matter below a square metre.

There are no data on which to base a similar estimate of the overall average population density of pelagic fish in the English Channel. All that can be done is to examine a presumption that it is not very different from that in the North Sea. The relative proportion of species is quite different; extensive and dense shoals of pilchard are encountered; great numbers of pilchard eggs are found in the water and further to the westward, in addition, an almost equal number of mackerel eggs. At first sight this suggests a mackerel population similar in over-all density to that of the pilchard. But this is not so, for pilchard eggs hatch out as larvae in a much shorter time than mackerel eggs. The herring fishery in the Channel has never been commensurate, area for area, with that in the North Sea. Although different shoaling habits of the fish could account for this, there is more reason to believe that the overall population density of

the fish is less in the Channel. The great difference between the two areas is the pilchard population, not present in the North Sea, and exploited in the Channel to only a limited extent on account of a restricted market for this fish. Recently a ship searching for shoals with an echo-sounder has encountered numerous shoals, some quite extensive, half a mile or more across. The fish, when shoaled, are sometimes so dense that they obliterate any 'trace' being recorded from sound reaching the sea bottom and returning to the ship. Furthermore, if a weighted wire is hung from a ship when over a shoal, fish are continually knocking against the wire. Fishing with a ring trawl, having a head rope 260 yards long and encompassing some 4600 m.^{2} of water, catches of 4800 kg. of pilchard or more have been obtained. These observations suggest that when in shoals, the population density may well amount to about 1 kg. of fish per square metre, containing 170 g. of organic matter.

This tentative estimate of the density of shoaled fish permits a calculation which suggests that 1·8 g. of organic matter per square metre in pelagic fish in the North Sea may not be very different from the overall density in the English Channel. On this assessment the mouth of the Channel, extending to some 10,000 square miles, would contain some 5×10^{10} g. of organic matter as pelagic fish. If these were all pilchard, and all in shoals at a density of 170 g. organic matter below a square metre within the shoal, the shoals together would cover 18 square miles. This computed 18 square miles of shoals assumes that all pelagic fish, mackerel, herring and pilchard of all sizes shoal with a similar density and are all present in shoals. They do not do so.

Since many shoals, composed of pilchard only, some extending over half a square mile or more, have been encountered by a single ship during the course of a few months, this total of 18 square miles is not wildly improbable.

The food required by the pelagic fish deserves consideration. Various experiments cited in the literature have shown that fish weighing 10 g. or more consume some 2 l. of oxygen daily per kilogram of body weight. Most of the experiments have been made at room temperature, which suggests somewhat less consumption at sea temperature. There is no indication that these fish were either starved or heavily fed, so their oxygen consumption under natural conditions, where they are slowly growing, is likely to be similar. The value indicates that 1–1¼% of their tissue is consumed daily, and that a commensurate quantity of their daily intake of food is completely broken down to carbon dioxide. Presumably most of the food eaten in excess of this quantity will be returned to the water either in the form of solids or as partly digested and soluble organic matter, which will serve as food for other organisms and for bacteria. Hence the pelagic fish below a square metre, containing some 1·8 g. of organic matter will, on the average, assimilate daily a quantity of organisms containing about 1¼% of this amount of organic matter, in order to make good respiratory losses. These fish do not live wholly on zooplankton, although this

constitutes a large part of their diet. For simplicity in this computation they are assumed to feed on zooplankton alone.

Experiments on the growth of plaice over protracted periods have a bearing upon these rough estimates. In order to maintain their weight, without loss or gain, they needed some $1\frac{1}{4}\%$ of their own weight of animal tissue to be supplied daily as food.

In nature the pelagic fish are growing very slowly indeed, compared with small organisms such as the zooplankton. A herring or mackerel, some few months old and weighing 5 g., will take some 3 years to attain a weight of 100 g., and thereafter increase in weight still more slowly. During the 3-year-period it will have lost by respiration some 750 g. of tissue and gained 95 g. by growth.

In this step in the food chain, herbivore to carnivore growing rather slowly to moderate size, only 10 or 11% of the assimilated food is converted to carnivore tissue, the other 90% being respired as carbon dioxide. Whereas in the previous step, phytoplankton to quick-growing herbivore, 70% of the assimilated food is converted to herbivore tissue, in spite of the more rapid respiratory loss.

These quantities relate to the quantity of food assimilated. In order to increase growth, progressively more food doubtless needs to be eaten than is assimilated. Dawes's (1930, 1931) experiments on the growth of plaice indicate this. A small female fish eating 1·9% of its own weight of mussel flesh daily gained an average of 0·06% daily; a small male fish eating $2\frac{1}{2}\%$ of its own weight of mussel flesh daily gained 0·25% of its own weight daily.

Bacteria in Suspension

No observations have been made of the number of bacteria in the waters of the English Channel; at off-shore positions in other areas there are usually found some 100 or less per cubic centimetre which are capable of growth on nutrient media. Such plate counts give minimal values of their population density, because the bacteria tend to attach themselves firmly to suspended particles or organisms, and a particle with several attached bacteria would only 'count' as a single organism. Allowing for this, it appears unlikely that the number in off-shore waters exceeds about 1000 per c.c., and that no more than 0·2 g. wet weight occur below a square metre in a water column 70 m. deep. Such a quantity would contain some 0·04 g. of organic matter.

Their numbers in the sea are limited by the great dilution of dissolved organic matter serving as food in the water, probably no more than 5 or 10 mg. per litre, about half of which appears to be in forms unsuitable as bacterial food. Their growth is also probably limited by the presence of bacteriostatic substances, whose presence in the sea has lately been confirmed, and by their being ingested by other organisms.

Marine bacteria, at our mean sea temperature, lose by respiration some

30% of their own weight daily, varying from species to species. Their food requirements are great, although their biomass is small. This estimate indicates that no more than some 0·013 g. of dissolved organic matter below a square metre are broken down to carbon dioxide by bacteria daily.

Demersal Fish

It is unknown what average weight of demersal fish lies below an acre of the English Channel, but it is possible to make a reasoned guess. The North Sea is not strikingly dissimilar in fertility to the English Channel, and for the North Sea extensive data are available.

Approximately half a million tons of demersal fish were landed each year during the 1930's. Of fish which were marked and put back in the sea, one-third were caught again within a year. Some lose their marks, others are not reported. This indicates that the total population of marketable demersal fish was about one million tons. Small fish of the same species which either passed through the meshes of the trawls or were thrown back perhaps amounted to an equal weight. In addition there are unmarketable species—particularly those which never grow big. A total population of three to four million tons of demersal fish of all species and sizes is not unlikely. This is equivalent to a mean population density of fish below a square metre containing $1\frac{1}{2}$ g. of dry organic matter.

The English Channel is almost certainly less populated than the North Sea. The landings of fish per acre are one-third of the landings from the North Sea, but it is less heavily fished. Statistics show that steam trawlers landed during the 1930's rather less demersal fish from the English Channel than from the North Sea per 100 hr. trawling.[1]

This suggests a mean population density in the English Channel containing 1–$1\frac{1}{4}$ g. of organic matter, below a square metre, or some 50 lb. wet weight per acre.

Experiment has shown that demersal fish of moderate size completely consume and respire as carbon dioxide about $1\frac{1}{4}$% of their tissues daily, and further that they need to assimilate this quantity of tissue daily to maintain their weight. They feed very largely upon the bottom fauna, and therefore may be expected to assimilate daily a quantity of this containing some 0·015 g. of organic matter, and to eat rather more.

The relatively small consumption by fish compared with that by zooplankton (p. 129) is notable. Most of the planktonic animals reach maturity and die within a few weeks, except the brood which lives through the winter. Fish reach maturity in 1–7 years, and a very few individuals may attain a great age; cod and plaice as old as 24 years have been caught.

[1] During the course of an hour's trawling our research vessel sweeps about 10 acres of the sea floor and catches on the average rather more than 160 lb. wet weight of fish large enough not to escape through the meshes of the net.

The Bottom Fauna

A considerable population of animals, live on, and buried in, the sea floor the majority obtaining food by creating a current of water from which plankton and detritus is filtered. The mechanisms for doing this are diverse in kind; many of the organisms lie buried and extrude a tube to the surface through which the water is passed. A smaller number live by passing soil through their guts and, from this, organic detritus and bacteria are utilized. A further small number, notably starfish and gastropods living on the surface, are carnivorous. In addition to these carnivores, demersal fish live on the epi- and in-fauna, and constitute perhaps the most effective group of predators. The crabs, prawns and amphipods living on the bottom are thought to be mainly scavengers, most of them making little demand on the living bottom fauna.

The population density of animals which live on, or burrow into, the bottom varies very much from place to place. There are areas where lamellibranchs such as *Spisula* or, near shore, where the common mussel cover the ground almost touching each other. Here there may be more than a kilogram of moist living tissue on a square metre, containing 150–200 g. or more of dry organic matter. On other areas there are found no more than 25 g. of living tissue containing some 5 g. of organic matter.

As methods of obtaining samples to a depth of about 6 in. have been developed, more and more animal life is being found in bottoms which contain only a rather sparse quantity on or near the surface. Large and aged bivalves are being found, buried, and having thick shells, not readily accessible to starfish and too well protected for their shells to be broken by most fish (N. A. Holme, private communication). The biomass of the fauna occupying sand, shell or gravel bottom appears to be composed largely of aged, slow-growing, buried individuals of the kind whose daily loss by respiration is slow.

With the exception of a small area near the land, where mud containing organic matter is deposited, there have been only a limited number of quantitative observations where the sea floor has been sampled to a depth of 6 in. or more. Based on these, an average of some 100 g. of living tissue in and on a square metre now seems a reasonable estimate. This will contain some 17 g. of organic matter. With the development of more efficient gear, and of under-water photography, a better picture of the biomass of the bottom fauna will be possible.

Of the many kinds of bottom-living animals, except the smallest, only a few are thought to be annual. Those constituting the major part of the biomass may live for several years. There is a worm in our aquarium 11 years old.

The results of numerous experiments on the respiration rate of various bottom-living animals provide data for a rough assessment of that part of their daily food which is completely consumed to form carbon dioxide. The food which is eaten but not completely consumed by an individual serves as food for other species. That part of it which is built up into living tissue of the

individual eventually provides food for predators or bacteria. One assumption has again to be made, namely that the animals used for experiment had not been starved, but contained or had recently contained food commensurate with that in their normal natural condition. This assumption would appear valid because the experiments did not aim at obtaining the basal metabolic rate and because the animals in many instances were collected shortly before the experiments.

The experiments, conducted between 16 and 23° C., show a very much greater respiration rate for small animals (around 200 c.c. of oxygen consumed per kg. of living tissue hourly) than for larger animals (around 80 c.c.). At our mean sea temperature the rates would be probably reduced to about two-thirds. Since the biomass of animals, when their population density is around 100 g. of living tissue per square metre, is mostly composed of larger slowly respiring animals, a mean rate of 80 c.c. oxygen consumed hourly per kilogram of tissue (170 g. of organic matter) is indicated. This implies the loss of $1\frac{1}{4}\%$ of their organic matter daily.

Hence organisms containing 17 g. of organic matter will assimilate 0·21 g. daily for their maintenance. There is no evidence that the population waxes and wanes with the seasons; however, the food to maintain the population will vary with the temperature of the water, although many of the organisms are likely to adapt their metabolism to slowly changing temperature.

It is remarkable that the population density of filter-feeding organisms on the sea floor should vary so greatly, often over extensive areas adjacent to each other, between which there is no reason to suppose the filter-feeders' food supply differs to any material extent.

Survival, particularly of the young, from predators, must play a considerable part in regulating the population density. For instance, an area in Plymouth Sound was heavily populated with mussels 4–5 cm. long in 1947, when *Asterias*, which had either settled there as larvae or had moved in from an adjacent area, decimated the population. However, it seems very improbable that the balance of life between carnivores and filter-feeding organisms can wholly account for the very different populations of the latter, except in isolated areas of limited geographical extent. Another instance of rapid change in bottom fauna in this vicinity does not allow any such simple explanation. An area of several square miles in Start Bay was very thickly populated with *Spisula*; within a period of some 2 months a heavy mortality took place, most of the *Spisula* shells sampled being then either empty or containing a dead organism; this catastrophic mortality had no obvious cause.

The nature of the sea floor has a marked influence not only on the species composition of the fauna, but also upon its density in terms of biomass. The former is readily understandable, the latter less so, for among the thousands of species of filter-feeding bottom-living organism, there must be many suited to life on or in all kinds of soils, with the exception of shifting sand which would

dislodge or bury their young. It is perhaps pertinent that under-water photography has shown ripple marks on sand at quite considerable depths, which suggests that the effect of gales may extend to depths hitherto unexpected.

The kind of sea bottom undoubtedly affects the settlement of larvae of particular species, and their metamorphosis. By partially filling bottles with soil from different sea bottoms and suspending them in the sea, Thorson concluded that planktonic larvae, which metamorphosed and settled, were able to choose their substratum. From experiment with the planktonic larvae of the worm *Ophelia*, Wilson showed that for metamorphosis and growth a clean sand was necessary with rounded grains about three times their own size. For these larvae, the size and shape of the interstices between the sand grains appears to render the bottom suitable or otherwise. Further investigation is now showing the influence of yet another factor. A species of the worm *Protodrilus* inhabits an area of shell-gravel. Remarkable experiments by Jägersten indicate that metamorphosis of these planktonic larvae is caused by a chemical substance which slowly dissolves out of this shell gravel, to which its distribution is limited. Experiment has also shown that low concentrations of copper promote the settlement and metamorphosis of ascidian larvae; these concentrations, though low, being several times greater than that usually occurring in sea water. The settlement, metamorphosis and subsequent growth of oyster larvae on different surfaces has been the subject of much investigation. This has led to the observation by Cole & Knight-Jones that they settle in greater numbers on surfaces where oysters have already settled than on comparable surfaces where settlement has not already taken place.

The distribution of the bottom fauna in soil communities, resulting in part at least from the exercise of choice by the larvae while members of the temporary plankton, causes another factor to affect the density of settlement or resettlement on the sea floor. Currents or drift of the water, which tend to change from time to time, may carry the larvae away from their suitable substratum. There is evidence of this happening in the Dogger Bank area.

In spite of these limitations to spreading and replacement of the population, it is still remarkable that the population density should vary so greatly.

Bacteria in the Sea Floor

Several estimates have been made of the number of bacteria in marine muds containing organic detritus, in which they are likely to be more numerous than in clean open-sea deposits. Their numbers fall off rapidly below the upper layer of mud.

In the limited area of mud lying off Plymouth, investigated by Mare (1942), counts by dilution and plating indicate some $\frac{1}{2}$ g. wet weight of bacteria per square metre, containing about 0·1 g. of organic matter. Owing to their rapid respiration, bacteria lose some 30% of their substance daily at sea temperature, the rate varying with different species. Hence the complete combustion of 0·03 g. of organic matter daily per square metre due to bacterial activities is indicated.

On the Quantity of Organisms Present, and their Daily Food Requirements

The mean quantity of organisms present throughout the year, per unit area over a considerable expanse of sea in the Plymouth sea-area, is set out in Table IV. Each quantity is deduced from the foregoing conclusions.

These rough estimates point to the pelagic organisms requiring vegetable food from which to assimilate some 0·23 g. of organic matter daily. There results from this intake zooplankton containing 0·15 g. of organic matter, a portion of which nourishes the pelagic fish, the remainder being eventually eaten by the bottom fauna.

Table IV. Mean Quantity throughout the Year of Plants and Animals below Unit Area, the Average Depth being 70 m.

Wet weight of tissue containing 80% of water per acre (lb.)	Type of organism	Dry weight of organic matter, g./m.²: Quantity below a square metre (g.)	Daily production per square metre (g.)	Daily loss due to respiration	Food assimilated daily (g.): Lost by respiration	Food assimilated daily (g.): Built into new tissue
?180	Phytoplankton	*c.* 4	0·4–0·5	—	—	—
70	Zooplankton	1·5	0·15	4%	0·06 vegetable tissue	0·15 vegetable tissue
80	Pelagic fish	1·8	[0·0016][1]	1¼	0·025 animal tissue	—
—	Bacteria	0·04	—	30	0·013 dissolved organic matter	—
50	Demersal fish	1–1·25	[0·001][1]	1¼	0·015 animal tissue	—
800	Epi- and in-fauna	17	[0·03][2]	1¼–2	0·2–0·3	—
—	Bacteria	0·1	—	30	0·03	—
				Total	0·34 to 0·44	

[1] Based on a natural mortality of 30% per annum, due to being eaten.
[2] Based on a natural mortality of 60% per annum, due to being eaten.

Thus half of the deduced daily production of vegetable tissue appears to be assimilated by plant-eating organisms in the water column, leaving the other half, together with 0·12 g. of zooplankton organic matter, to maintain the bottom fauna, including the demersal fish feeding upon it.

In this table the zooplankton, assessed as containing 1·5 g. of organic matter per square metre on the average throughout the whole year, has been treated as entirely herbivorous. This it never is, and on rare occasions there may even be a considerable proportion of carnivores for short durations of time. On account of this alone, the relative proportion of plant to animal tissue available for the bottom fauna will vary. Furthermore, the ten per cent daily production is taken as persisting throughout the whole year, whereas it slows in winter. In consequence the estimate is more likely to be high than low.

Nevertheless, these observed and computed quantities shown in Table IV

indicate the dominant part played by zooplankton as consumers of vegetation and providers of food for animals higher in the food chain. They indicate that the production of zooplankton (0·15 g. daily or 2200 lb. wet weight per acre yearly) exceeds the production of all other animals.

The total daily loss by respiration of the whole animal community (0·34–0·44 g. of organic matter) is slightly less than the deduced daily production of organic matter. No significance is attributed to the total of the crudely estimated animal and bacterial requirements being rather less than the even more crudely estimated production of vegetable organic matter. Yet one might expect some loss of organic matter due to oxidation taking place in the sea without the agency of bacteria or other organisms. Experiments by Keys, Christensen & Krogh (1935) on the oxygen consumption by bacteria in stored sea water lends credence to an expectation of some non-vital oxidation in the sea.

The various estimates of production and losses have been arrived at in the following manner. On pages 118 and 124 computations have been made of the percentage of assimilated food which is converted into additional tissue in the growing animal. These relate to a steady population where the daily accretion is either eaten by other animals or fished by man—where growth equals the yield. Then

Food assimilated in unit time (f)
= growth in unit time (g) + respiratory loss in unit time (r).

The validity of these computations depends upon having chosen values of g and r for a sea temperature around 12° C. which are representative of whole populations, embracing all ages in terms of biomass, not of numbers. The premises have been stated from which these values, relating to a community of herbivorous zooplankton, were derived. Much the greater part of the biomass of a community of fish consists of individuals of moderate size—over 10 or 20 g.—such as have been found to lose $1\frac{1}{4}$% daily by respiration. There will be some fully grown, increasing not more than about 20% by weight annually (2–3% in linear dimensions) and respiring rather less rapidly. There will also be a small proportion by weight of quite small fish respiring more rapidly. For the whole community a loss by respiration of 1·25–1·5% daily appears a reasonable mean value. The growth rate, which, under the circumstances postulated, equals the rate of yield and the rate of mortality, is thought to lie in the region of 30–50% per annum for the major part of the biomass, much more for the small portion of it composed of quite small fish and less for the older larger fish. This indicates a growth rate of 0·08–0·14% per day. Observations of the bottom fauna indicate that most of the biomass is composed of well-grown organisms, many of considerable size. Even in the mud investigated by Mare, only 1% of the biomass consisted of micro- and meiobenthos. Well-grown bivalves and worms have been found to lose about 1–1·25% daily in respiration, quite small organisms very much more.

If, as a rough approximation, about a quarter or a third by weight of the bottom fauna is assumed to lose 4% daily on an average, and the remainder $1\frac{1}{4}$%, the whole community loses 2% daily. Concerning the rate of yield or mortality of this community, most of the biomass consists of long-lived animals feeding on vegetable and zooplankton detritus, many having attained an age of several years. A mortality rate of 60% of the biomass per annum seems a not unreasonable conjecture.

On these premises Table V is also constructed. It suggests that every 100 g. of vegetable tissue assimilated may yield:

70 g. of herbivorous short-lived zooplankton.
11 g. of herbivorous well-grown long-lived bivalves or worms.
4–7 g. (6–10% of 70 g.) of pelagic fish feeding on herbivorous zooplankton.
1 g. (6–10% of 11 g.) of demersal fish feeding on well-grown bivalves.
0·3 g. of carnivore feeding on carnivore, as fish on fish; or more if both are small and short lived.

It is implied that all the animal food eaten by carnivores is assimilated.

TABLE V. BALANCE SHEET OF ANIMAL PROTOPLASM

	Percentage loss of biomass per annum 'Annual Mortality'	Percentage increase daily by weight (g)	Percentage loss daily by respiration (r)	Percentage of food assimilated, which is built into new tissue $\left(\frac{100g}{g+r}\right)$
Zooplankton herbivores	—	10	4	70
Fish, community of all ages	30 50	0·08 0·14	1·25–1·5 —	5–6 8½–10
Bottom fauna, most of the biomass being well-grown individuals	60	0·16	2	11
Full-grown fish, bivalves or worms, increasing in tissue weight not more than 20% per annum	—	<0·05	1–1·25	<5

Although the premises on which these computations are founded are not sufficiently exact for definite quantitative conclusions to be drawn, they provide or expand a series of implications, most of which are self-evident without any such quantitative reasoning. Thus the yield, derived from the same quantity of primary vegetable food, will be still further reduced for every step in the food chain, if the food supply is inadequate. The average age, and the size, of individuals constituting an ecological group will have a profound effect upon this yield: if the respiration rate is doubled or the growth rate halved, the effect upon this yield will be the same, hence a higher sea temperature may be partially offset by an increased growth rate. The yield of pelagic

fish feeding on herbivorous plankton will be greater than that of demersal fish feeding on slowly growing bivalves, provided that both can collect a sufficiency throughout the whole year.

In addition to the losses which occur for every step in the food chain, there is a deterioration of food every time an organism is eaten or mutilated, due to organic matter passing into solution and becoming useless as food except for bacteria and possibly for some protozoa.

The estimates shown in Tables IV and V, and computations based on them, can only be accepted as pointers and not as conclusions, only as a first attempt to envisage the changing life in the sea as a whole and on a roughly quantitative basis. The estimates themselves are rude, but they are not notional, being founded on observation and experiment.

These estimates envisage the sea maintaining an average of 1000 lb. of animal tissue per acre. Is this quantity surprisingly great? The food chain leading up to many of the animals is long and this is not conducive to great fertility. On the other hand, it appears to be animals larger than bacteria and protozoa which convert most of the plants and each other into carbon dioxide. This constitutes a great difference between life in the sea and on land, where a proportion of the vegetation nourishes a considerable soil fauna of bacteria and protozoa. On the other hand, rich pastures may also maintain, out of sight, as much as 600 lb. per acre of worms and much insect life (Evans, 1948).

With a better 'balance of life' there is reason to suppose that the sea could maintain and yield an almost phenomenal quantity of animals compared with cattle on land. The Chinese have evolved a system where shallow sea-areas are banked off and filled with water from which predatory animals have been screened out. After the growth of algae has started, the 'ponds' are stocked with the fry of a quick-growing herbivorous fish. In the Phillipines, as described by Frey (1947), and also on the coast of India, this system is yielding as much as 5000–7000 lb. of fish per acre annually. At intervals of not more than 2 years, the ponds are drained and the mud bottoms allowed to bake in the sun; also, in India, they are ploughed. This treatment presumably affects the interchange of nutrient salts between soil and water, allowing more to pass into solution and preserve the pond's fertility.

Evidence of Changing Fertility

The term 'fertility' of a sea-area, in its wide sense, implies the annual production of plants and the average quantity of animals maintained in it throughout the seasons. This quantity includes the bottom-living and migratory animals; neither of these allow quantitative sampling with any exactitude. It also includes the planktonic life in the water mass which does not usually remain in the area for any length of time, and is always subject to being replaced by another of very different biological history and potentialities.

The term 'fertility' comprises three concepts:

(i) The production of plants rather than their population density. Since, in most areas, production is directly dependent upon the supply of nutrients throughout a part of the year, the potentiality of the water to supply these nutrients is an almost direct measure of fluctuation in plant production from year to year. This potentiality to supply depends upon physical factors—as turbulence and temperature, changing with the seasons and varying from area to area—and the water's content of total combined nitrogen and phosphorus. Hence the concentration of one or other of these in the water provides a measure of the *potential fertility of the water mass* with respect to its production of plants.

(ii) The population of animal plankton living on the plants, changing with the seasons and providing food for the carnivorous plankton. This whole population of animals and plants moves in and out of a sea-area with the water masses. Short-term fluctuations in the phytoplankton and in the herbivorous zooplankton assuredly affect the early survival of most other animals, for which they are the only food during larval life. The quantity of planktonic life in the water also affects, or often affects, the movements of the migrating pelagic fish.

(iii) The population of longer lived animals which, once established, are able to withstand rather long periods of starvation. Where the bottom fauna is abundant it is notable that the greater proportion by weight is composed of relatively large and aged animals, and this also holds for the fish. This established population, which appears to comprise more than half the weight of living organisms, will be least subject to immediate changes from fluctuations in food supply due to changing water masses in the area. Their early stages, however, and the chances of this population maintaining itself by renewal, is very dependent upon the supply of planktonic food. The larvae need a population of food suited to their particular need, a population of organisms sufficiently dense for the larvae to be able to catch enough, a population present throughout the whole early life of the larvae. It is during their larval life that their respiration rate is greatest and they have not sufficient food reserves to live through an interval of starvation.

From general observations in the Plymouth area there is little doubt that the quantity of both pelagic and bottom-living organisms has decreased during the past 30 years. This opinion is not founded on measurement, but it is reinforced by the results of sampling and measuring particular populations and conditions.

Since 1924 comparable hauls have been made at weekly intervals with a stramin net, having meshes with openings around 1×1 mm., each haul filtering roughly 4000 m.^{3} of water. During 1924, 1926 and 1929, consistently heavy catches were made, containing considerable quantities of late-stage copepods and euphausians. During 1925 and 1927 the catches were much less: during

subsequent years, particularly recently, catches have been very sparse indeed. It was soon observed by Russell that a relation existed between the size of the catches and the phosphate in the water at the beginning of each year.

The numbers of young fish in the catches were recorded. Of these, the number of clupeid fish varied in a very irregular manner in the daytime, and many more were caught at night (Russell, 1930). Hardy records catches of 2448, 27, 7, and 341 young herring in comparable vertical hauls, at intervals of a few hours, at substantially the same position in the North Sea. The numbers of young demersal fish, caught in each haul in this area, present a more regular picture.

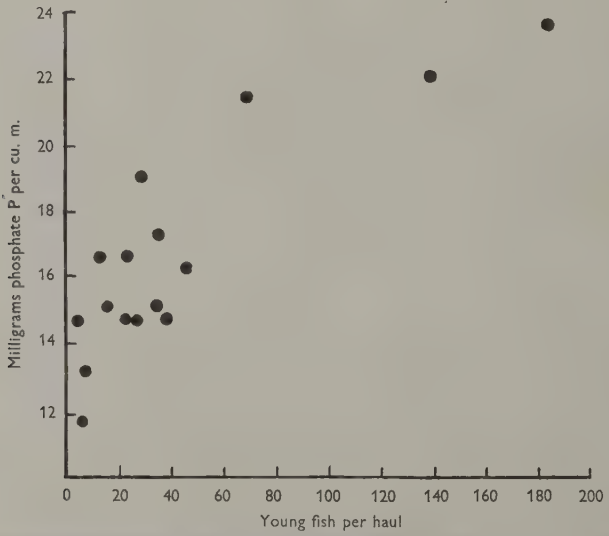

Fig. 10. Relation between the number of young fish caught per haul and the phosphate in the water occupying the area during the previous winter.

The average number caught between June and October are plotted against the concentration of phosphate in the water at the beginning of each year in Fig. 10. These numbers relate to fish spawned in summer, after the spring outburst of phytoplankton, and after the peak population of planktonic crustaceans which immediately follows it. These young fish lived their early life during a season when food was not at its greatest seasonal abundance.

At about the time when these fish larvae have absorbed their yolk sac, or very shortly after, they need to catch small crustacean or other larvae. This is a most critical period of their lives, when great mortality occurs. Observations by Rollefsen show that the food organisms need to be below a certain size. If unable to pass down a fish's gullet with an effective diameter of 0·2–

0·3 mm. they choke the fish. If organisms of small enough size are not sufficiently numerous, an increasingly large proportion of the larval or post-larval fish fail in their attempts to catch food during the critical period, and so perish. A major cause of good or bad survival years for young fish would appear to be the population density of zooplankton organisms of the right size at the right time.

There are three steps in the food chain between the young fish which have survived the post-larval stage and the quantity of plant nutrients. Furthermore, the quantity of nutrients in winter may sometimes bear no relation to the production of plants in the area during summer, on account of a different water-mass with very different potential fertility having meanwhile entered the area. In spite of this, *the highest winter concentrations of phosphate are seen to have marched with the most considerable survival of post-larval fish during the following summer, and the least winter concentrations of phosphate with the least survival.*

Another relation appeared during the course of these observations. The rich plankton populations found in the nineteen-twenties contained *Sagitta elegans* in considerable numbers, whereas in the sparse populations this species was replaced by *S. setosa*. During a cruise in 1935 there appeared to be a rather sharp line of demarcation between plankton-rich water containing *S. elegans* and plankton-poor water containing *S. setosa*. Thus it emerged that, like the winter concentration of nutrient salts, the presence of some plankton species marched with the quantity of the whole planktonic population.

There are observations made during 3 years which allow a comparison of the quantity of the larger phytoplankton organisms in the water. Frequent vertical hauls with a net of 0·05 × 0·04 mm. mesh, containing a meter, were made at the same position. The results expressed in terms of plant pigments per cubic metre (Harvey, Cooper, Lebour & Russell, 1935, p. 419, and fig. 12, p. 424) indicate a lesser population of these larger plants in 1949 than in 1934, and lesser in 1934 than in 1933. The quantity of phosphate in solution in the water during the previous winters varied in the same way (13, 15 and 16 mg. P per cubic metre respectively) although the differences were not great. The average number of post-larval fish, exclusive of clupeids, caught in 4000 m.^{3} of water between June and October also varied in the same way (10, 16 and 23 fish per haul). Standing alone, this close relation between winter nutrients, larger plants, and summer-spawned young fish, would mean little, since it only embraces 3 years.

Observations of the population of smaller zooplankton (copepods and copepodites) extend over 2 years only, 1934 and 1939. Neither the quantity of zooplankton, the number of young fish in summer nor the winter phosphate were notably dissimilar.

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THE SUSPENDED MATTER OF SEA WATER

By F. A. J. Armstrong and W. R. G. Atkins, F.R.S.

From the Plymouth Laboratory

Many chemical analyses have been made of the minor constituents of sea water which are utilized by plants and accordingly show definite seasonal variations. Analyses have also been made of the plankton strained out by fine-mesh silk nets. According to Harvey (1945) the finest bolting silk used, when wet and swollen, has a mesh of $42 \times 50 \mu$. This will let through the dwarf or nanoplankton, namely the smaller flagellates and diatoms, also bacteria, at least until the net is partially choked, as well as the finest clay particles, if any are still unprecipitated. Clay usually comes down close to the land, due to the action of the divalent magnesium and calcium ions of sea water as shown by Joly (1900).

Method of Sampling

An attempt to measure the amount of these suspensions, living, dead and inanimate was made as follows. Carboys of sea water were filled at Station E 1, about 10 miles south-west of the Eddystone, in the English Channel, where the depth is 72–74 m. The water was taken in a carefully scrubbed and washed oak bucket, poured in through a clean wooden funnel, under the eye of the authors. The water surface was always free from oil and care was taken that the rim of the bucket should not touch the side of the ship, which sometimes had dried mud remaining on it above the wetted portion.

The carboys used were well washed with hot lime-free tap water and finally with distilled water, as customary here, and closed with a clean cork sealed in position. It was found that some of the suspended matter adhered to the glass, so during filtration it was loosened with a brush, which was then well washed. After the first four samples we considered that the customary cleaning of the carboy was likely to leave some of this matter on the glass. So from June 1948, inclusive, the carboys were cleaned with hot strong sulphuric acid in addition. The analyses for February to May 1948 show that this adherence of previous deposits gave results which were too high, but the matter removed was similar in composition to the usual suspension.

Filtration and Determination of Dry Matter

The volume of sea water filtered varied, as some was used for other analyses, but lay between 15 and 29 l., with a mean close to 22. It was filtered through a Whatman No. 50 paper, 11 cm. diameter, the ash of which, 0·2 mg., was negligible. This was done on a Buchner funnel with the water pump. The first 10 l. was always re-filtered.

As a test of the efficiency of the filtration sea water collected 8 November 1949 was first filtered as usual; 25·0 l. gave 24·7 mg. or 990 mg./m.^{3} of incinerated matter. Then 22·0 l. of the filtrate were filtered through 'Gradocol' membranes having an average pore diameter 1·09 μ. As these became clogged four had to be used in succession. The washed residue and the filters were ignited and gave 0·9 $\pm$ 0·2 mg., or 40 mg./m.^{3}, of which gravimetric analysis showed that 60% was silica, and ferric oxide 13%, found colorimetrically using 2–2′-dipyridyl.

Thus the filter-paper, with re-filtration as described, allowed about 4% of the matter to pass through, which was later collected on the membrane. The appearance and composition of the fine suspended matter on the membrane were similar to that on the paper. Examination in the Tyndall beam showed that there was still matter in suspension in sea water filtered in succession through 'Gradocol' membranes 1·09, 0·61 and 0·2 μ A.P.D., but the amount must have been exceedingly small by weight.

After washing free from salts the residue was also washed with 20 ml. portions of acetone till colourless, and dried at 100° C. The net weight is that of organic and inorganic matter, insoluble in water and acetone. But only occasionally was there enough on the paper to render this weighing worth while, as it is necessarily less accurate than that of the incinerated residue.

The paper was incinerated below red heat till carbonaceous matter was destroyed. The ratio of the organic matter to the inorganic and ash was 0·68 in July 1948 and 1·01 in February 1949. In March, April and May 1948 the imperfectly cleaned carboys gave respectively the ratios 0·91, 1·82 and 0·31, but the March and April samples were not filtered till $4\frac{1}{2}$ and $3\frac{1}{2}$ months after collection.

The values for July 1948 and February 1949 give the insoluble organic matter as 1·77 and 1·62 g. dry weight for a cubic metre of water at the surface. This is a direct determination, but may be low on account of the loss of soluble substances.

The July 1948 ratio, 0·68, is moreover low, as on this occasion the inorganic matter was enriched with calcium carbonate which constituted 70% instead of about 20%. The high calcium content is probably due to high temperature and pH value, which combine to cause precipitation.

The incinerated dry matter is shown in the table as mg./m.^{3} The constituents are shown both in mg./m.^{3} to afford a comparison with analyses of the salts in solution and in percentages, using the oxide formulae as customary in the analyses of clays in agricultural work and in the Challenger analyses.

Gravimetric Analysis of the Residue

Silica was determined by the loss of silicon tetrafluoride. The factor to correct to Si is 0·467.

Iron was found by fusion of the residue with potassium hydrogen sulphate, followed by acid extraction, formation of the cupferron complex and its extrac-

tion with chloroform. The solvent was removed and the complex destroyed with sulphuric acid and heat, followed by hydrogen peroxide, solution in acid and ammoniacal precipitation when just alkaline to methyl red. The precipitate was ignited and weighed as Fe_2O_3; the factor to convert to Fe is 0·700.

Aluminium was precipitated in the aqueous solution after the cupferron extraction by addition of ammonium chloride and then hydroxide till just alkaline to methyl red. The precipitate was ignited and weighed as Al_2O_3. The factor to convert to Al is 0·529.

The filtrate from the aluminium determination was freed from ammonium salts, organic matter if present being destroyed with hydrogen peroxide. Calcium was then precipitated as oxalate, and ignited and weighed as the carbonate. The factor to convert to Ca is 0·400.

One determination of phosphorus was made on a duplicate carboy of 30 November 1948. In view of the acid extraction necessary later on this was filtered on a Jena grade 3 (medium porosity) sintered glass crucible. With refiltration of the first 10 l. this proved efficient, and gave 2100 mg./m.^{3} residue dried at 100° C. Cold extraction with 0·28 N-H_2SO_4 gave 3·1 mg./m.^{3}, and hot extraction (in autoclave, Harvey, 1948) gave a further 2·2 mg. The residue when incinerated and extracted gave 0·2 mg., so total phosphorus in residue was 5·5 mg./m.^{3}

Since the other carboy gave 950 mg./m.^{3} incinerated residue a further value for the organic/inorganic matter ratio is obtainable, namely 1·21 and the insoluble organic matter is 1·15 g./m.^{3} The samples of water may not have been identical in the two carboys, but are likely to have been closely similar.

Discussion of Results

The results are given in Table I. Neglecting results from inadequately cleaned carboys the incinerated dry matter ranges from 2·77 to 0·45 g./m.^{3}, namely parts per million, with silica as the main constituent in all but four cases. In one of these calcium carbonate, probably from the sea, constituted 70%.

The silica may have three origins: silica as such from diatom tests, silica fairly pure from small sand grains and apparently buoyed up by organic matter, and silicates of aluminium and iron, namely clay, brought down by rivers.

Incinerated dry matter varied from 100 to 16; the silica from 100 to 9; the iron oxide from 100 to 20; the aluminium oxide from 100 to 7. The greatest variation in silica was, very strangely, between 8 and 17 August 1949, with 80 and 880 mg./m.^{3} respectively. As against this Atkins (1926) found silica in solution at E 1, 0 m., to vary from 240 to 40 mg. between 1923 and 1926. It appears, therefore, that the silica in suspension must—from the aluminium figures—be largely present as silicate and capable of enriching water depleted by diatom growth by slow solution. There is, however, no sign of any regular seasonal change in the silicate. The figures appear quite fortuitous. Nor do

TABLE I. WEIGHT OF SUSPENDED MATTER IN 1 M.^{3} OF SEA WATER, SHOWN AS INORGANIC MATTER AND ASH, AFTER INCINERATION, IN MILLIGRAMS, EQUIVALENT TO PARTS PER THOUSAND MILLION

The major constituents are shown, also the percentage composition. The years are 1948, above, and 1949.

Date	Weights (mg.)					Composition (%)					° C.	Salinity (‰)
	Total	SiO_2	Fe_2O_3	Al_2O_3	$CaCO_3$	Total	SiO_2	Fe_2O_3	Al_2O_3	$CaCO_3$		
11 Feb.	1,060*	465	96	81	250	85	44	9	8	24	10·1	35·27
10 Mar.	6,770*	3,700	740	1,300	630	95	55	11	20	9	9·3	35·35
12 Apr.	6,900*	3,100	650	810	1,360	86	45	9	12	20	10·2	35·33
10 May	15,300*	7,900	—	1,800	2,400	80	52	—	12	16	12·4	35·46
9 June	1,140	520	130	70	200	89	54	11	6	18	12·6	35·34
15 July	2,770	700	86	<20	1,900	99	25	3	<1	70	14·7	35·34
16 Aug.	890	380	130	50	160	82	43	15	6	18	15·4	35·34
4 Oct.	490	220	60	60	90	88	44	12	13	19	14·7	35·37
30 Nov.	950	160	140	140	200	73	17	21	14	21	13·2	35·38
5 Jan.	760	160	160	130	190	84	21	21	17	25	11·2	35·35
1 Feb.	1,600	420	250	160	310	71	26	15	10	19	10·2	35·27
1 Mar.	740	160	130	80	90	62	21	17	11	13	10·1	35·38
13 Apr.	800	300	100	90	190	84	37	13	11	23	9·9	35·27
9 May	800	250	180	80	110	77	31	23	10	13	11·5	35·32
9 June	1,360	710	110	150	250	89	52	8	11	18	13·9	35·30
8 July	1,880	770	300	270	310	88	41	16	14	17	16·5	35·41
8 Aug.	450	80	120	70	110	89	18	28	16	27	15·3	35·43
17 Aug.	2,020	880	260	160	490	89	44	13	8	24	16·0	—
29 Aug.	800	340	120	90	240	98	42	15	12	29	19·4	—
6 Oct.	590	260	150	60	100	92	43	24	9	16	16·4	35·25
8 Nov.	1,190	520	210	190	310	103	44	17	16	26	14·0	35·26

* Inadequately cleaned carboys.

delays in the filtration of the carboys appear to cause any serious error, for filtration of the 8 August sample was begun on 16 August and that of 17 August on 20 August.

On the whole, the aluminium values appear to be low in the summer, giving the impression that it might be the more soluble. The amount of iron present in suspension was far more than that found in solution by Cooper (1935). Atkins (1945) showed that the reduction in silica in solution due to diatom production was only about 10% of that which should have been found had all the phosphate used gone to diatom production. The present demonstration of another source of silicate does tend to lessen this discrepancy, but can hardly be accepted as adequate to account for the great difference. One is thus justified in thinking that the non-siliceous phytoplankton may be quite important quantitatively.

Summary

Sea water collected at Station E 1, surface, between June 1948, and November 1949, contained suspended matter from 2·77 to 0·45 g./m.^{3} (or parts per million) dried and ignited. A few determinations of insoluble organic matter gave 1·77 to 1·15 parts per million dry weight at 100° C. The ignited residue contained from 55 to 17% silica, 28 to 3 of ferric oxide, 20 to under 1 of alumina and 70 (or excluding one high value 29) to 9 calcium carbonate. There was nothing in the records for temperature or salinity to suggest that the water mass had changed during the period of sampling.

The analyses reveal an unsuspectedly large amount of iron, compared with that found in solution. The ignited residue is rich in silicate, judging from the silica alumina ratio, but it is quite doubtful whether the additional supply of silicate available for diatoms is at all adequate to balance their requirements calculated on a phosphate utilization basis. It seems more probable that a considerable amount of the phosphate is available for non-siliceous phytoplankton.

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THE CYCLE OF PHOSPHORUS IN THE WATERS OF THE ENGLISH CHANNEL

By F. A. J. Armstrong and H. W. Harvey, F.R.S.

From the Plymouth Laboratory

(Text-figs. 1–10)

A study of the distribution of phosphorus compounds—in solution in the water, in planktonic, in free-swimming and in bottom-living organisms, in detritus and in deposits on the sea floor—forms a natural sequence to two groups of observations which have been made in recent years. The one group has shown that water masses have been present in the mouth of the English Channel containing very different concentrations of phosphate in winter, when the phosphate concentration reaches a maximum—concentrations ranging from 10 mg. phosphate-P per cubic metre in some water masses to over 20 mg. in others. The second group of observations has shown a great difference in the population density of macroplankton between one water mass and another, and, also, more macroplankton and a better survival of young fish in the waters off Plymouth during years when the winter maximum of phosphate in the water was greatest.

The aim of this present study is twofold: towards finding a constituent of sea water which is unaffected by seasonal changes and whose concentration differentiates one water mass from another, and towards a further insight into those factors which affect the fertility of an area of the sea and cause fluctuations in population during the course of years.

Most of the data have been collected at a distance of 20 miles off shore from Plymouth in a depth of 70 m. The water occupying this area does not stay there; as shown by changes in salinity, it is replaced by other water masses at frequent and irregular intervals. Since it is impracticable to follow one particular water mass in its wanderings and intermingling throughout a year, seasonal changes in a particular water mass cannot be determined directly. From observations at one position small seasonal changes may not be apparent and could be demonstrated only by a series of observations taken at one position throughout many years, sufficient for fluctuations due to changing water masses to iron themselves out.

On the other hand, the considerable seasonal changes which occur in phosphate, nitrate, phyto- and zooplankton are quite apparent. They outweigh fluctuations arising from a succession of water masses passing through the area.

The earlier attempts to estimate organic phosphorus compounds in solution in the sea were vitiated by the use of a method of analysis which included in

the estimate any arsenate present (Kreps & Osadchik, 1933; Kalle, 1933; Seiwell & Seiwell, 1934).

This analytical difficulty was overcome by Kalle (1935, 1937), who then surveyed a considerable area of the southern North Sea in the winter of 1935. He envisaged the probability that the total phosphorus in dissolved compounds was a distinction between water masses—'Hilfsmittel zur Unterscheidung von Wasserkörpern'.

His investigation showed very different concentrations of total phosphorus and of phosphate in January in different areas of the North Sea. It also showed that the more turbid waters contained large quantities of this element in suspension.

During the same year, another analytical method was devised by Redfield, Smith & Ketchum (1937), which also eliminated interference by arsenic. They estimated phosphate in solution, total phosphorus and phosphorus in particulate matter retained on a filter, at a position in the Gulf of Maine on five occasions during a year, to a depth of some 250 m.

The position lay in a water mass which is considered subject to but little interchange with the surrounding water. During the course of the year, there was no marked difference in the total phosphorus in the water column between summer and winter.

	May 1935	Aug.	Nov.	Feb. 1936	May
Total P, grams below a square metre	9·4	10·1	10·7	9·8	11·0

Their research showed that the integral mean concentration of total phosphorus in a water column could be used to distinguish one water mass from another at any time of year.

A series of total phosphorus estimations have also been made in the nutrient-poor waters of the Adriatic, at intervals throughout a year, using Kalle's method (Nümann, 1941). The data provide no indication of any seasonal change in the total phosphorus content, but the quantity is very small, averaging 5 mg. P/m.^{3}, compared with over 30 mg. in the Gulf of Maine, 12 mg. off Plymouth during recent years and, by inference, over 20 mg. during the relatively rich period some 25 years ago.

The main difficulty in further investigation lay in the uncertainties inherent in the technique of estimation. Even the estimation of dissolved phosphate at great dilutions embraces reactions which are imperfectly understood; this is indicated by several papers appearing every year on modifications of the molybdenum blue method.

An examination has been made of the reactions involved in phosphate estimation and, also, a more simple and rapid variant of the method used by Redfield *et al.* to estimate total phosphorus in water samples has been developed (Harvey, 1948; Armstrong, 1949). The sample is acidified to 0·28 N and heated for 5 hr. at 130° C.; this treatment in the presence of chloride appears to hydrolyse all or almost all the organic phosphorus compounds; any

arsenate present is reduced with sulphite. Large quantities of arsenate may be added to the sea-water sample without showing any increase in the estimate of total phosphorus.

On the other hand when a sample of sea water is analysed for inorganic phosphate, the estimate by molybdenum blue includes the equivalent of any arsenate which may be present in the water. This amount is unknown.

Analyses of English Channel waters have shown the presence of some 19 mg. As per m.^{3} (Orton, 1923), which compares with 7–24 mg. in more recent analyses of Atlantic waters (Rakestraw & Lutz, 1933) and 15–38 mg. in Pacific waters (Gorgy, Rakestraw & Fox, 1948). The latter authors found that from 8–16% of the whole existed as arsenate.

Based on the value of 19 mg. As/m.^{3} in English Channel waters, this suggests that 1·5–3 mg. may be present as arsenate. These quantities would appear in the estimated concentration of phosphate as 0·6–1·2 mg. P of phosphate-P actually present.

Some experiments made during this investigation are of interest. When sea water is autoclaved with acid, as in the estimation of total phosphorus but *without added sulphite*, any added arsenite is oxidized to arsenate. This treatment would also be expected to disrupt any organic arsenic compounds, which are likely to be present in sea water because many marine organisms concentrate arsenic in their tissues.

Thus the difference in molybdenum blue developed in waters which have been acidified and autoclaved with and without added sulphite, gives an indirect measure of the arsenic present. Estimations in waters collected off Plymouth in 1947 gave values amounting to 3·1, 2·6 and 2·4 mg. As/m.^{3}, in a water collected in 1948 only 1 mg. As, and in a composite sample collected in 1949, 2·1 mg. As, there being less in the same water after filtration.

These were unexpectedly low values, in view of the direct estimations of total arsenic made in England and America by the methods of Marsh and Gutzeit respectively.

Some further observations made during this investigation suggest that little or no arsenite may be present as such in the sea. When a solution of sodium arsenite was added to samples of sea water at pH 8–8·2, increasing the concentration by 40 mg As/m.^{3}, it was oxidized to arsenate. This happened rapidly in some waters, slowly in others.

We do not know what proportion of the estimated values of phosphate-P are due to arsenate; there is conflicting evidence of how much to expect.

Since June 1947 samples taken from a series of depths, at the position 20 miles off-shore, have been analysed for phosphate and for total phosphorus.

Distribution of Phosphorus in the English Channel

In winter, 20 miles off-shore from Plymouth and elsewhere in the English Channel, both phosphate and total phosphorus remained almost constant throughout the water column. Filtering the water had negligible effect—the quantity of phosphorus in particulate form is then very small indeed. Replicate samples taken from the same depth show only small differences between each other. The distribution shown in Fig. 1 is typical of winter conditions in this area; phosphate-P accounts for some 90% of the total.

Fig. 2 is derived from the data by Redfield *et al.* in the Gulf of Maine. Here there appears to be a different water mass below 170 m., in which practically all

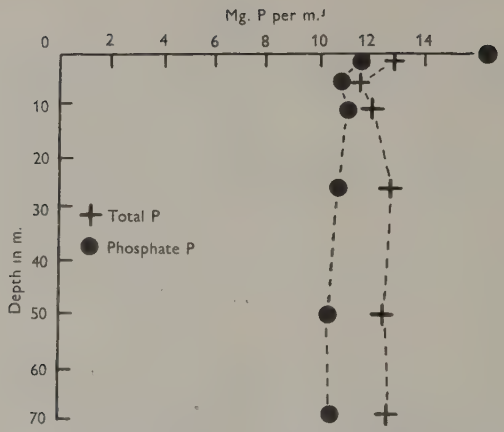

Fig. 1. Distribution of total and of phosphate-P in the water, 20 miles off shore, 5. i. 49. Depth 70 m.

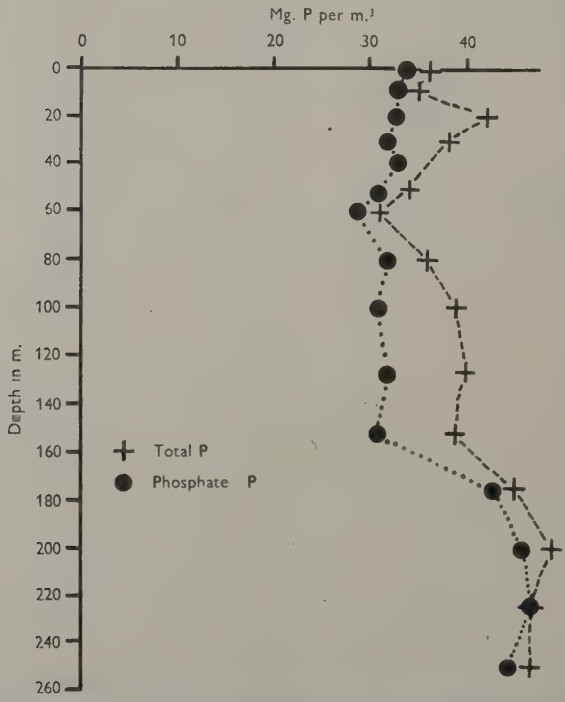

Fig. 2. Distribution of total and of phosphate-P in the Gulf of Maine, 26. ii. 36. From data by Redfield, Smith & Ketchum (1937).

the organic phosphorus has reverted to phosphate, whereas above 170 m. phosphate-P accounts for some 90% of the total.

In the waters so far investigated at the time of the winter phosphate maximum, the phosphate in the water columns amounts to 85–90% of the total phosphorus.

During the winter months, in particular, there is an odd phenomenon which we have frequently observed. If the water sample is taken from the surface, it often contains rather more total phosphorus and more phosphate than occurs in the water below. The cause is not obvious; possibly dust from the atmosphere may become trapped by surface tension at the air surface, or particles in suspension may attach to themselves minute bubbles of air during rough weather when waves are breaking, and these, rising to the surface, become entrapped. Both Söderstrom (1924) and Wilson (1932) have observed that when larvae of *Polygordius* and of *Owenia* come into contact with the surface they are held there and even torn apart by the surface forces. Suspended matter removed by filtration from water collected at the surface of the sea was rich in phosphorus. On two occasions it accounted for 5·5 and 2·2 mg. P/m.^{3}.

As the year advances, some redistribution takes place. Phosphate is used by the plants in the upper layers. Zooplankton, rising into these layers at night, graze on the plants and retiring by day excrete phosphate and soluble organic phosphorus compounds into the water below. Thus, until June, organic phosphorus compounds increase at the expense of phosphate. Most of this increase is in the form of dissolved organic P, since the quantity of phosphorus in the plankton never increases beyond a small fraction of that in solution. Also throughout the summer, there is less total phosphorus in the upper layers, due to vertical transport by plant-eating zooplankton, than in the water below. In several of our observations in summer there was a slight but significant accretion of phosphorus between 20 and 40 m. depth.

From February to June in 1948 and 1949 the dissolved organic plus particulate phosphorus increased from 10 or 12% to some 65% of the total in the 70 m. water column off Plymouth. A typical distribution is shown in Fig. 3, while Fig. 4 shows the distribution in the deeper water of the Gulf of Maine in August.

In order to determine the very small quantity of phosphorus present in particulate matter in suspension, samples were collected at regular intervals of depth and mixed to give a composite sample, representative of the whole water column. Part was filtered through No. 42 Whatman paper. From this and the unfiltered remainder, replicate subsamples were taken for analysis. The difference between the mean values for the filtered and unfiltered samples gave a measure of the phosphorus in particulate matter. Table I shows the results of these analyses; it also includes the calculated quantity of phosphorus present in zooplankton and plants. The data from which these values were derived are given in a separate communication (Harvey, 1950, pp. 97–137).

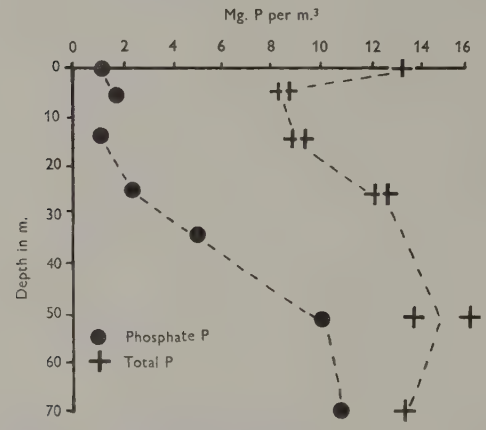

Fig. 3. Distribution of total and of phosphate-P in the water 20 miles off shore, 31. viii. 48. Depth 70 m.

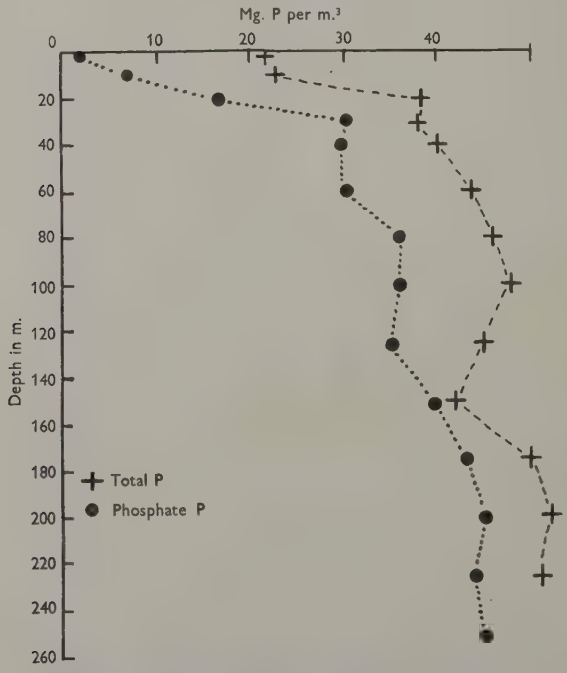

Fig. 4. Distribution of total and of phosphate-P in the Gulf of Maine, 21. viii. 35. From data by Redfield, Smith & Ketchum (1937).

By subtracting the quantity in living plankton from the total, a rough estimate is obtained of the quantity in detritus. This is thought to be mostly organic detritus, fragments of once-eaten diatoms and zooplankton, which can be seen present in the water after the spring flowering of diatoms in early April.

TABLE I. ANALYSES OF TOTAL P, MG. PER M.^{3}, IN COMPOSITE SAMPLES FROM 20 MILES OFF-SHORE

	1. iii. 49	13. iv. 49	9. v. 49	9. vi. 49	6. vii. 49	8. viii. 49	8. ix. 49	8. xi. 49
Unfiltered	15	16·4	14·9	11·6	11·7	11·0	12·8	12·1
	13·7	16·9	14·7	12·1	11·9	10·2	12·1	12·5
	13·3	15·6	14·1	11·9	12·0	9·6	12·9	12·6
		15·5	12·6	11·8	11·6	10·3	12·4	13·1
		16·3	14·6	12·0	12·4	9·0	12·3	15·5
		16·2	14·6	11·9	12·5	10·4		13·8
			14·6					
Av.	14·0	16·15	14·3	11·9	12·0	10·1	12·5	13·3
Filtered	13·3	14·8	11·3	9·7	10·5	9·1	11·9	13·1
	13·6	14·7	11·4	10·0	10·4	8·5	12·2	13·7
	13·5	14·6	11·7		10·7	8·9	12·0	
		14·9	11·2		10·4	8·9		
Av.	13·5	14·75	11·4	9·9	10·5	8·9	12·03	13·4
P in particulate matter (by difference)	0·5	1·4	2·9	2	1·5	1·2	0·45	—
P in phyto-plankton	0·13	0·42	0·78	0·5	<0·5	<0·5	<0·4	—
P in zooplankton	0·2	0·8	1·0	0·5	0·5	0·5	0·4	—
In detritus (by difference)	0·2	0·2	1·1	1·0	0·5	0·2	—	—

The nature of the particles of inorganic phosphate likely to occur in turbid waters is of interest. Dietz, Emery & Shepard (1942) have described sedimentary deposits of calcium phosphate, containing fluoride, which were laid down off the Pacific coast of America. They conclude that sea water is fully saturated with respect to calcium phosphate. Cooper (1948*a*, *b*) considers that particles in suspension are likely to consist of ferric phosphate, which is one of the most insoluble phosphates, and that these particles, once formed, may hydrolyse somewhat slowly in sea water. As a statistical average, waters richer in iron were also richer in phosphate.

With regard to this possibility, the following experiment is of interest.

Ferric phosphate was prepared and very thoroughly washed. The addition of this to a culture of phosphate-starved diatoms was followed by a prolific growth; this also happened when it was enclosed in a cellophane sac and suspended in the culture.

When added to sea water in a stoppered vessel, the pH quickly fell to *c.* 7. The water was poured off and replaced, the pH of this fresh sea water fell in the same way. The fall in pH of successive replacements of sea water became progressively slower.

The conclusion arrived at was that hydrolysis takes place at pH 8, becoming infinitely slow at *c.* pH 7, and that the rate of hydrolysis is much greater the finer the particles.

In addition to the estimates made in waters 20 miles off-shore, estimations have been made from time to time at positions nearer Plymouth. Sometimes there was rather less phosphorus in the water and at other times more. The distribution in January 1949 is shown in Fig. 5, when a 'richer' water lay nearer the shore. The high concentrations occurring in water collected from the surface on this occasion are noteworthy.

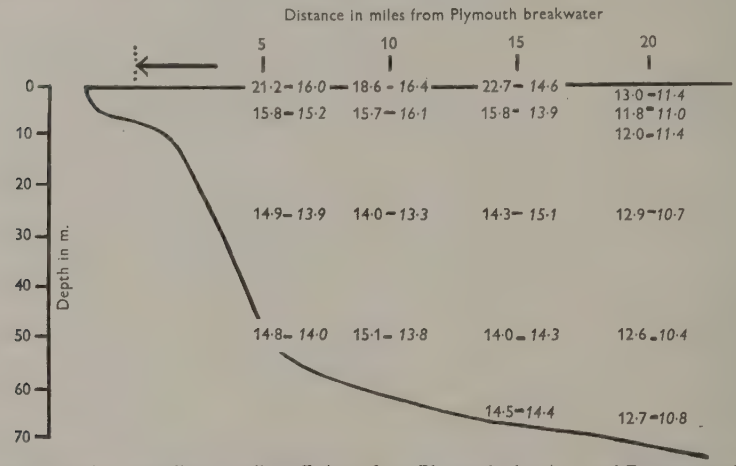

Fig. 5. Section extending 20 miles off-shore from Plymouth showing total-P concentration (upright type) and phosphate-P (italics) in mg./m.^{3}. 5 and 14. i. 49.

The integral mean concentrations of total and phosphate-P in the whole water column at the position 20 miles off-shore are shown in Fig. 6.

The total has fluctuated in an irregular manner between $9\frac{1}{2}$ and 16 mg. P/m.^{3}, while the salinity of the waters sampled fluctuated between 35·0 and 35·4 $^0/_{00}$.

No relation is apparent between the fluctuations in total phosphorus and in salinity.

It is thought that the fluctuations in total phosphorus are almost entirely due to richer or poorer water moving into the area. Yet it is, of course, possible that incursions of water have by chance masked a seasonal change in phosphorus content. Only a series of observations extending over many years would rule out this possibility.

Further evidence bearing upon a possible seasonal variation was therefore sought in two directions: (1) whether organic detritus is deposited on the sea floor after the spring maximum of planktonic life and slowly regenerates phosphate; (2) whether the quantity of phosphorus locked up in living organisms which die during the autumn and winter months is at all considerable. Neither

inquiry provided evidence indicating a material seasonal change in the total phosphorus in the water.

It was considered that if any deposition of organic matter takes place, it would lie on the sea floor as a sludge or slurry. Therefore an apparatus was constructed which sucks in water from close to the bottom very rapidly. A strong spring is released when the foot of the apparatus touches bottom, retracting a piston which sucks in water with a rush. Fitting a longer foot allowed samples also to be taken from 35 cm. above the bottom.

Samples taken close to the bottom contained a little organic detritus and a little silt in addition to sand grains. Their phosphorus content was little greater than that in samples taken from water above (Table II). No evidence was found of any material deposition of detritus rich in phosphorus.

TABLE II. TOTAL PHOSPHORUS IN WATER SAMPLES OBTAINED BY 'PISTON SAMPLER' FROM CLOSE TO THE BOTTOM

12. v. 48		23. vii. 47	
20 miles off-shore	mg. P/m.^{3}	13 miles off-shore	mg. P/m.
5–6 cm. above bottom	16·5, 14·5	5–6 cm. above bottom	18·0, 24·0
35 cm. above bottom	12·4	35 cm. above bottom	14·7
5 m. above bottom	16·6, 11·6	3 m. above bottom	14·2
25 m. above bottom	9·6	8 m. above bottom	13·1
50 m. above bottom	10·3		
29. ix. 47		29. ix. 47	
13 miles off-shore	mg. P/m.^{3}	5 miles off-shore	mg. P/m.^{3}
5–6 cm. above bottom	14·2, 11·4	5–6 cm. above bottom	11·4, 15·7
35 cm. above bottom	11·4	15 m. above bottom	14·0
3 m. above bottom	10·2	25 m. above bottom	13·6, 12·1
16 m. above bottom	10·7		

Computations of the phosphorus in fish and bottom fauna, as incorporated in Fig. 10, amounted to a fifth of the whole below a square metre. Since these animals probably grow most rapidly in spring and early summer a quite small seasonal variation of phosphorus, dissolved and suspended in the water, is indicated.

The data for the mean integral concentration of total and of phosphate-P in the water column, presented in Figs. 6 and 7, permits the ratio of phosphate to organic phosphorus in the water column to be calculated on each occasion when a series of samples had been collected and analysed. This ratio is shown in Fig. 8. Except for a single occasion, the seasonal change in the ratio has followed a remarkably constant course.

On this exceptional occasion, 9 June 1949, the percentage of phosphate was greater than a month earlier or a month later. The changes in salinity and temperature which had occurred provided no explanation of this. It is thought that there had moved into the area a body of water in which plant life had been less abundant during the previous 3 months.

It is seen from Figs. 7 and 8 that, from the end of January until June, the

rate at which organic phosphorus compounds are being excreted is greater than the rate at which they are changing into phosphate. The most rapid increase in dissolved organic phosphorus took place in March and April, when production of plants was at its height; it ceased some time in June when the temperature was rising rapidly and organic detritus in suspension had reached

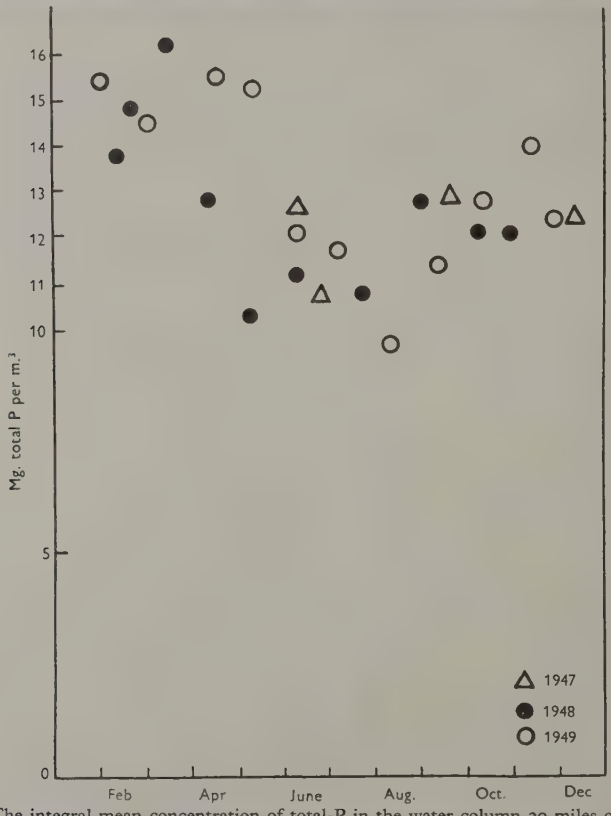

Fig. 6. The integral mean concentration of total-P in the water column 20 miles off shore.

a maximum. The increase ceased and phosphate started to increase long before the temperature of the sea reached its maximum in August.

There is no evidence whether breakdown of organic phosphorus compounds is mostly due to slow chemical decomposition or to bacterial action. If the latter, a seasonal variation in numbers of bacteria in the water would be indicated. This is not unlikely, because they grow rapidly on any surfaces such as those presented by particles of detritus in suspension.

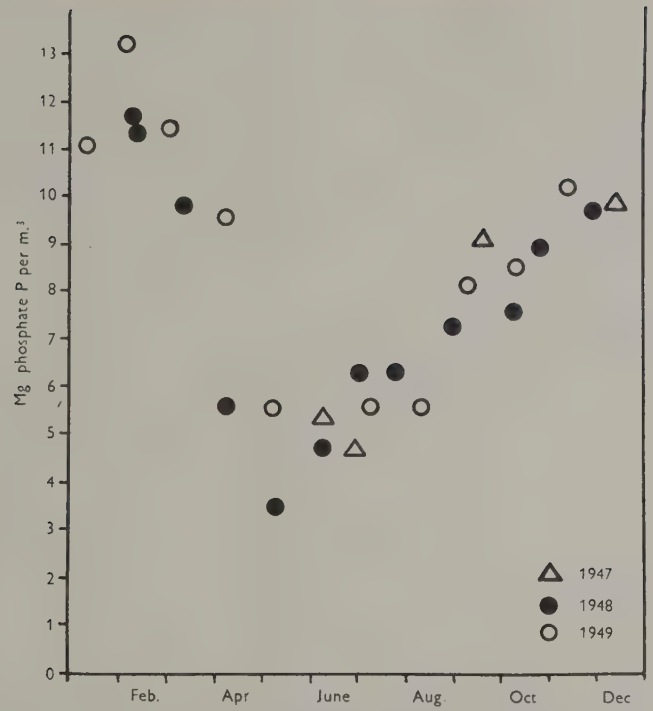

Fig. 7. The integral mean concentration of phosphate-P in the water column 20 miles off-shore.

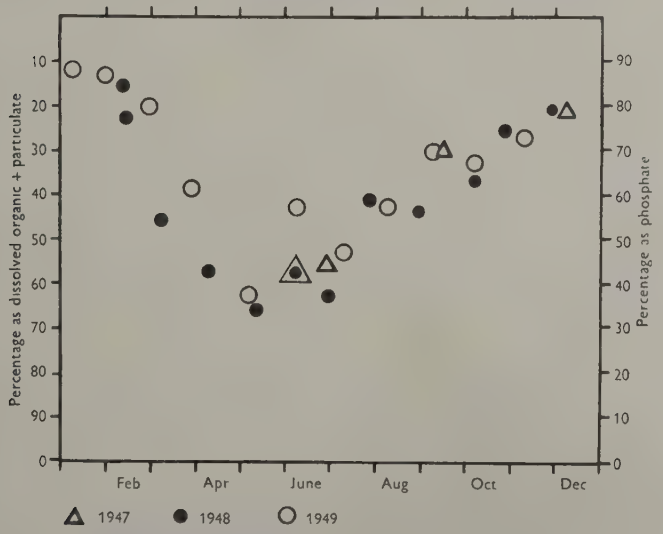

Fig. 8. Diagram showing the seasonal variation in the percentage composition of the phosphorus in the water column 20 miles off-shore.

There are difficulties in investigating the breakdown of organic phosphorus under natural conditions. If a sample of water is brought into the laboratory, conditions for such changes are entirely altered. The number of bacteria rise from a few hundred per c.c., or less in water well off-shore, to several million per c.c., the number of species falling. The surface of the container becomes coated with bacteria.

Distribution of Phosphorus elsewhere in the English Channel

In January 1947 areas of the sea were traversed during a cruise to the south and west where the water contained from 12 to 18 mg. phosphate-P/m.^{3} The areas with the highest content lay some 60 miles and some 120 miles to the westward of Plymouth (Cooper, private communication). Since then we have sampled water columns in the western part of the Channel with an average content of as little as 10 mg. 'total' P/m.^{3} and as much as 23 mg.

Hence fluctuations in the total phosphorus content of the water column off Plymouth may be expected, as different water masses drift through the area.

All the estimates so far considered have been in waters which are clear and transparent, free from organic detritus, and in which a Secchi disk is visible to a considerable depth.

Distribution of Phosphorus in Turbid Waters

The turbid waters of the southern North Sea present a different picture from those in the western English Channel. They contain a very material quantity of phosphorus in the form of detritus, as has been shown by Kalle (1937) in January—as much as 40–50 mg. P/m.^{3} at some inshore positions, and negligibly small quantities in some of the central and of the least turbid areas.

We are indebted to Mr R. S. Wimpenny for samples from the southern North Sea, taken in June and August. Fig. 9 shows the large quantity at an inshore position. The concentration increases with depth, in spite of the water being well mixed by tidal streaming, and it increases hand in hand with the turbidity of the water.

Another sample from a similar position showed that a material proportion of the phosphorus in the suspended detritus consisted of solid inorganic phosphates (Harvey, 1948). Some of this dissolves in the dilute acid in which phosphates are estimated, and, in consequence, appears in analyses as dissolved phosphate.

On the Distribution of Phosphorus Between Water, Animals and Plants

Any study of the cycle of phosphorus in the sea necessitates some knowledge of how much is present in plants and animals.

Observations of the phosphorus in the zooplankton below a square metre of the sea, some 5 miles off Plymouth, the depth being 50–55 m., had been made

throughout 1934, and that of the larger net-caught phytoplankton throughout several years. The quantities present below a square metre were very similar to those 20 miles off shore, in a depth of 70 m., where most of the chemical data have been obtained. There were no observations concerning the smaller phytoplankton which escapes capture in a net having meshes of $42 \times 51\ \mu$ and a great capacity for entangling smaller diatoms, nor concerning the average population density of fishes or of bottom-living organisms.

This necessitated an inquiry, the results of which are presented separately (Harvey, 1950, pp. 97–137). Estimates, based on direct observation, of the quantity of phyto- and zooplankton below a square metre are incorporated in Table I (p. 151).

Fish are both migratory and unevenly distributed; available data allow no more than a conjecture of the average quantity in the western part of the English Channel.

The bottom-living animals are also very unevenly distributed, and the number of quantitative observations in the area are relatively few and over a limited area. These allow no more than a probable conjecture of the average population density—some 100 g. wet weight of living tissue below a square metre, the bulk of this being in animals having a life span of several years and living by filter-feeding on plankton organisms and organic detritus.

These estimates are incorporated in Fig. 10, which indicates the distribution of phosphorus in a water column, 70 m. deep, as investigated during 1947–49. This is roughly the average depth of the western part of the English Channel.

No seasonal change in the quantity of pelagic and demersal fish is shown, on the assumption that month by month the rate of replacement of the biomass by growth balances losses by mortality. The quantity of bottom-living organisms, the infauna and epifauna, is also delineated as constant throughout the seasons, on the same assumption.

However, a large proportion of these bottom-living animals discharge planktonic larvae during the spring and early summer, larvae which contribute to the zooplankton, although not forming a large part of it, having only a short planktonic period and being for the most part soon eaten by other planktonic organisms. This discharge of larvae into the water is accompanied by a material loss of the parents' body substance, and suggests that the water is likely to contain a little more dissolved phosphorus during the spring and early summer, perhaps as much as 1 mg. P/m.^{3} This possibility is compatible with the values for total phosphorus shown in Fig. 5.

While considering the distribution between water and organisms, the state and quantity of phosphorus in bottom deposits deserves mention.

Muds rich in organic matter are laid down in estuaries, as those in the Clyde, Tyne and Tees which are rich in phosphate and, presumably, organic phosphorus. Their phosphate content decreases with depth, indicating slow solution into the overlying water. Conditions affecting solution in such a mud

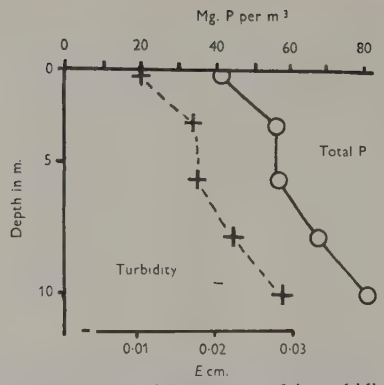

Fig. 9. Diagram showing change in total-P content and in turbidity with depth in turbid water. Samples collected off the Newcombe Bank, southern North Sea, June 1947. Depth 12 m.

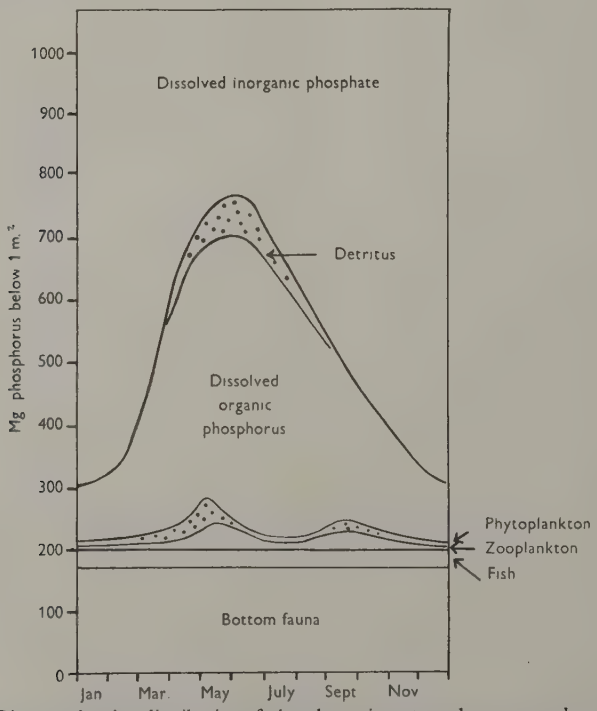

Fig. 10. Diagram showing distribution of phosphorus in water column 70 m. deep, Plymouth area. (Phosphorus in solution and in detritus based on observations made in 1948 and 1949, in zooplankton based on observations made in 1935 farther in-shore, in fish and bottom fauna on computations, Harvey, 1950, pp. 97–137.)

have been studied by Stephenson (1949). These mud deposits occupy very restricted areas and are quite different from the floor of the open sea.

Yet, well off shore, the deposits are not devoid of phosphate. A fine silt or grey mud collected several miles off shore was found to contain 0·03 % P—less than in soils, but a considerable quantity if any of it dissolves during the course of years.

The possibility of some small interchange between inorganic deposits and water cannot be dismissed.

Phosphorus Content and Fertility of Water Masses

The foregoing observations indicate that different water masses can be distinguished, one from another, by their total phosphorus content. Where, however, a water mass of less than 50 or 70 m. depth overlies a different water mass, the distinction may be difficult, since the zooplankton cause a redistribution in the upper layers during summer.

The observations also show that geographical distribution in terms of total phosphorus content does not coincide with the distribution in terms of salinity. There is also evidence that the total phosphorus content bears a relation to the productivity and general fertility of the water.

Evidences of the dependence of the animal population upon the supply or production of plant life, and of the latter upon the supply of nutrient salts, is reviewed on pages 132 to 135.

That the supply of phosphate varies with the total phosphorus in the water is implicit from the foregoing observations.

Hence it is expected that the mean concentration of total phosphorus in the water column denotes the potential fertility of the water occupying any particular area of the sea, its changing concentration providing a measure of changes from month to month and year to year in the supply of nutrient to the phytoplankton. It also appears to bear a broad relation to the population density of zooplankton which the water does maintain. An exact linear relation cannot be expected.

Observations of total phosphorus in the sea are limited, and comparable quantitative assessments of the population almost equally so. However, the observations summarized in the two following paragraphs point to this broad relation between total phosphorus in the water and the animal population maintained in it.

For a long period hauls have been made weekly off Plymouth with a ring trawl of 1 mm. mesh, each oblique haul filtering some 4000 m.^{3} of water. It was observed that the catches of macroplankton, including young fish, were particularly heavy during 1924, 1926 and 1929, and that the winter maximum of phosphate at the beginning of each of these years was particularly high (Russell, 1935). This suggested that the water, rich in nutrient salts, was not displaced by noticeably poorer water during the first 8 or 9 months of each of

these years: it also suggested that a rich phytoplankton resulted in a rich zooplankton and good survival of young fish. In Harvey, 1950, fig. 10 (p. 134 of this *Journal*) is plotted the average number of young fish, exclusive of clupeoids, caught per haul from June to October, against the phosphate maximum at the beginning of each year. A marked relation is seen, in spite of water movements having assuredly taken place between winter and summer on many occasions.

During the summer months in the Gulf of Maine, where the water contains over three times more phosphorus than the water off Plymouth has contained since 1947, the average phytoplankton population during the summer months is considerably greater than in the water off Plymouth. The zooplankton below a square metre averaged during the summer months between 9 and 20 g. dry weight, compared with 1–2 g. in the waters off Plymouth (Riley & Bumpus, 1946).

Several other observations, which point towards this broad relation, are presented or are implicit in the considerations dealt with on p. 135.

We acknowledge with gratitude the assistance of Dr L. H. N. Cooper, Mr G. A. Steven and Mr P. G. Corbin, who collected for us many samples for analysis when on cruises in the Channel.

Summary

Determinations of total phosphorus in water samples have shown areas in the western English Channel with water containing as little as 10 mg. P/m.^{3}, and other areas with double, and more than double, this concentration.

The integral mean concentration of total P in the water column, 20 miles off-shore from Plymouth, has fluctuated between 10 and 16 mg. P/m.^{3} since June 1947.

The changes which have taken place in this integral mean concentration are attributed to different water masses, of different total phosphorus concentration, passing through the area, rather than to a seasonal change in the total phosphorus content of a water mass. No marked deposition of phosphorus-containing detritus could be found.

Changes in this integral mean were not coincident with changes in salinity. The geographical distribution of total phosphorus does not coincide with the geographical distribution of salinity.

In winter, 85–90% of the total phosphorus is in the form of dissolved inorganic phosphate, which fell to 45% of the total in the early summers of 1947–49.

The ratio of (dissolved inorganic) phosphate to organic phosphorus (in solution and in particles) has followed a regular seasonal change.

There is some diminution of total phosphorus in the upper 20 m. layer in

summer. This is attributed to zooplankton feeding in this layer by night and excreting some of their intake when they retire by day into deeper water.

Estimates have been made of the proportion of phosphorus in solution, in detritus, in plankton and in other animals.

At positions closer in-shore the water sometimes contained a little more and sometimes a little less total phosphorus.

Water collected from the surface of the sea was frequently richer in phosphate, and in total phosphorus, than water from below the surface.

Evidence is presented that the total phosphorus in the water distinguishes one water mass from another, is a measure of its potential fertility, bears a relation to the annual production of vegetation and of zooplankton, and also bears a relation to the survival of post-larval fish spawned in summer.

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	Depth (m.)	Total-P (mg. P/m.^{3})	Phosphate-P (mg. P/m.^{3})	Difference
		9. vi. 47		
Position 50° 02′ N., 4° 22′ W., 20 miles SSW. from Plymouth breakwater (International Station E 1)	0·5	9·1	2·0	7·1
	10	10·2	2·3	7·9
	25	13·8	9·2	9·6
	50	13·0	7·4	5·6
		30. xi. 48		
	0·5	15·5	10·2	5·3
	5	11·3	9·9	1·4
	10	12·3	9·5	2·8
	25	12·7	9·6	3·1
	50	12·0	9·1	2·9
	70	11·9	10·6	1·3
		18. vi. 47		
Position 1–2 miles SW. of Eddystone, 10 miles SSW. of Plymouth breakwater	0·5	11·9	2·2	9·7
	5	12·3	2·5	9·8
	10	12·4	4·2	8·2
	15	11·8	2·9	8·9
	20	12·5	3·1	9·4
	25	13·3	3·8	9·5
	30	12·5	4·8	7·7
		18. i. 47		
Position 49° 50′ N., 7° 15′ W. Sounding 120 m.	5	22·9	18·6	4·3
	25	22·6	19·8	2·8
	50	22·6	19·6	3·0
		9. iii. 49		
Position 50° 36′ N., 8° 04′ W. Sounding 70 m.	5	21·4	15·8	4·6
	25	23·6	15·5	8·1
	60	24·5	15·2	9·3

	Depth (m.)	Total-P (mg. P/m.^{3})	Phosphate-P (mg. P/m.^{3})	Difference
		28. vi. 47		
	0·5	8·3	3·2	5·1
	5	8·5	1·9	6·6
	10	7·9	2·5	5·4
	15	9·5	2·1	7·4
	20	12·3	3·6	9·7
	30	10·2	4·2	6·0
	40	12·3	5·6	6·7
	50	10·0	7·9	2·1
	60	10·1	5·8	4·3
		5. i. 49		
	0·5	13·0	11·9	1·1
	5	11·8	11·0	1·8
	10	12·0	11·4	0·6
	25	12·9	10·7	2·2
	50	12·6	10·4	2·2
	70	12·7	10·8	1·9
		23. vii. 49		
	5	10·2	2·3	7·9
	10	11·6	2·2	9·4
	20	12·3	5·0	7·3
	30	12·6	6·5	6·1
	40	11·8	7·4	4·4
	50	13·1	6·8	6·3
	65	14·2	6·8	7·4
Position 49° 38′ N., 5° 20′ W. Sounding 90 m.				

	Depth (m.)	Total-P (mg. P/m.^{3})	Phosphate-P (mg. P/m.^{3})
		18. ix. 47	
	0	11·6	4·9
	5	11·3	4·9
	15	13·2	8·1
	25	13·5	7·8
	50	13·0	9·0
	69	13·1	9·0
		1. ii. 49	
	0·5	15·6	13·6
	5	14·8	13·1
	10	15·3	12·8
	25	15·5	13·2
	50	15·5	13·8
	70	14·8	12·5
		29. ix. 47	
	5	10·7	4·7
	15	10·1	5·1
	25	10·5	5·1
	50	10·7	6·1
	63	10·2	6·1
		28. vi. 47	
	5	6·5	1·9
	10	8·6	1·6
	15	7·3	6·1
	20	12·3	4·9
	40	11·0	10·4
	50	11·8	7·0
	80	11·4	8·7
		10. iii. 49	
	0	17·0	11·5
	5	16·4	11·8
	20	16·8	11·8
	40	18·0	11·5
	60	18·3	12·1
Position 3·5 miles N. of Longships lighthouse. Sounding 70 m.			

TABLE III. DETERMINATIONS OF TOTAL AND OF PHOSPHATE-P IN W

Difference	Depth (m.)	Total-P (mg. P/m.³)	Phosphate-P (mg. P/m.³)	Difference
		10. xii. 47		
7·6	0	13·3	10·0	3·3
7·3	5	13·3	9·5	3·8
5·1	25	13·2	9·8	3·4
6·7	50	13·5	10·1	3·4
4·0	70	13·3	9·5	3·8
4·1				
		1. iii. 49		
2·0	0	16·7	13·3	3·4
1·7	5	13·8	11·6	2·2
2·5	10	14·4	11·4	3·0
2·3	25	14·6	11·3	3·1
1·7	50	14·7	11·6	3·1
2·3	70	14·5	11·3	3·2
		24. xi. 47		
6·0	10	11·3	8·4	2·8
5·0	60	11·8	8·8	3·0
5·4				
4·6				
4·1				
		Position 49° 22′ N., 6° 12′ W. Sounding 119 m.		
4·6				
7·0				
1·2				
8·3				
0·6				
4·8				
2·7				
		Position 49° 44′ N., 8° 50′ W. Sounding 89 m.		
5·5				
4·6				
5·0				
6·5				
6·2				

Depth (m.)	Total-P (mg. P/m.³)	Phosphate-P (mg. P/m.³)	Difference
	12. ii. 48		
0	19·2	11·4	7·8
5	14·5	12·2	2·3
25	14·8	11·0	3·8
50	14·3	11·6	2·7
69	15·5	11·1	4·4
	13. iv. 49		
0·5	17·3	8·7	6·6
5	15·4	9·7	5·7
15	15·5	9·5	6·0
25	16·3	9·6	5·7
35	15·5	9·2	6·3
45	15·7	9·4	6·3
55	16·2	10·2	6·0
65	13·7	9·8	3·9
	22. xii. 47		
10	11·5	9·4	2·1
60	11·5	9·5	2·0
	28. vi. 47		
0·5	8·8	1·9	6·9
5	7·2	1·1	6·1
10	7·5	2·2	5·3
15	7·5	1·9	5·6
20	7·2	1·6	5·6
30	13·2	7·6	5·6
40	11·4	9·4	2·0
60	11·5	8·5	3·0
80	11·9	8·1	3·8
110	12·1	8·8	3·3
	3. v. 49		
0·0	11·7	3·1	8·6
5	10·4	5·2	5·2
20	10·4	3·6	6·8
40	14·0	4·7	9·3
80	19·4	12·5	6·9

Depth (m.)	Total-P (mg. P/m.³)	Phosphate-P (mg. P/m.³)	Difference
	11. iii. 48		
0	15·0	7·5	7·5
5	15·8	8·7	7·1
15	16·6	10·9	5·7
25	17·0	10·9	6·1
50	16·0	10·1	5·9
70	16·5	10·6	5·9
	9. v. 49		
0	10·1	2·0	8·1
5	8·9	1·1	7·8
15	7·7	1·9	5·8
25	12·0	3·2	8·8
35	16·4	8·4	8·0
45	18·3	8·0	10·3
55	18·4	8·3	10·1
65	17·6	8·5	9·1
	16. i. 48		
10	16·0	13·6	2·4
50	14·7	12·1	2·6
	30. vi. 48		
0·5	—	1·9	—
5	11·2	1·2	10·0
25	10·2	2·2	8·0
50	21·4	13·6	7·8
75	23·8	14·6	9·2
107	20·0	15·8	4·2
	12. vii. 49		
5	6·4	2·7	3·7
20	7·2	2·7	4·5
30	8·2	3·9	4·3
40	17·2	16·1	1·1
80	16·3	15·6	0·5
100	—	16·8	—
110	16·5	—	—

Depth (m.)	Total-P (mg. P/m.³)	Phosphate-P (mg. P/m.³)	Difference
	12. iv. 48		
0	10·1	4·8	5·3
5	15·4	5·4	10·0
25	12·6	5·5	7·1
50	13·1	7·0	6·1
70	12·8	5·1	7·7
	9. vi. 49		
0·5	9·7	4·8	4·9
5	9·0	4·7	4·3
10	10·5	4·7	5·8
20	12·7	5·7	7·0
25	14·6	10·8	3·8
30	13·4	10·8	2·6
40	12·5	10·8	1·7
50	12·9	10·8	2·1
60	13·3	10·1	3·2
68	13·0	10·0	3·0
	10. i. 49		
0·5	22·7	14·6	8·1
5	15·8	13·9	1·9
25	15·1	14·3	0·8
50	14·3	14·0	0·3
58	14·4	14·5	—
	Position 50° 00′ N., 7° 10′ W. Sounding 110 m.		
	Position 49° 28′ N., 6° 30′ W. Sounding 119 m.		

Total-P (mg. P/m.³)	Phosphate-P (mg. P/m.³)	Difference	Depth (m.)	Total-P (mg. P/m.³)	Phosphate-P (mg. P/m.³)	Difference	Depth (m.)	Total-P (mg. P/m.³)	Phosphate-P (mg. P/m.³)	Difference	Depth (m.)	Total-P (mg. P/m.³)	Phosphate-P (mg. P/m.³)	Difference	Depth (m.)	Total-P (mg. P/m.³)	Phosphate-P (mg. P/m.³)
12. v. 48				8. vi. 48				1. vii. 48				29. vii. 48				31. viii. 48	
—	1·2	—	0·5	8·5	1·5	6·0	0·5	12·0	1·2	10·8	0·5	16·1	1·8	14·3	0	13·5	1·1
8·5	2·1	6·4	5	10·7	2·2	8·5	5	12·0	0·3	11·7	5	7·8	1·3	6·5	5	8·5	1·7
14·6	4·0	10·6	25	10·3	2·8	7·5	25	20·6	7·4	13·2	25	9·1	4·7	4·4	15	9·0	1·1
10·3	3·4	6·9	50	12·4	8·4	4·0	50	16·7	9·6	7·1	50	13·0	9·5	3·5	25	12·7	2·4
9·6	4·0	5·6	70	11·8	8·4	3·4	70	16·2	9·6	6·6	70	12·1	10·0	2·1	50	15·0	10·4
11·6	4·6	7·0													70	14·0	11·1
6. vii. 49				11. vii. 49				8. viii. 49				8. ix. 49				6. x. 49	
8·3	2·6	5·7	5	5·8	3·9	1·9	10	8·5	3·4	5·1	0·5	—	4·8	—	0·5	12·9	7·1
8·3	3·5	4·8	20	7·6	3·1	4·5	20	9·7	4·3	5·3	5	—	3·6	—	5	12·7	5·9
8·9	2·3	6·6	30	11·9	6·8	5·1	30	8·9	—	—	10	8·1	4·2	3·9	10	12·2	5·4
14·0	5·7	8·3	70	10·5	7·1	3·4	40	9·5	—	—	20	13·9	—	—	25	12·7	8·9
12·7	6·5	6·2					50	10·0	7·0	3·0	30	11·3	—	—	50	12·7	10·1
11·2	6·9	4·3					60	10·4	—	—	40	11·3	—	—	70	12·7	9·1
11·2	6·9	4·3					70	9·9	6·8	3·1	50	11·5	9·2	2·3			
11·2	7·0	4·2									60	12·2	—	—			
12·2	8·1	4·1									70	10·8	9·9	0·9			
				29. ix. 47				12. ii. 48				11. iii. 48				27. vii. 48	
1 50° 15′ N.,			10	15·6	5·8	9·8	25	16·3	11·5	4·8	5	16·7	9·9	6·8	5	7·8	3·1
W., 6 miles SSW.			30	12·8	4·8	6·0					50	19·4	13·3	6·1	25	10·4	5·9
mouth breakwater			50	14·0	7·5	6·5									40	12·3	9·1
				11. x. 48								12. x. 48					
ition 50° 05′ N.,			5	—	5·3	—	Position 50° 00′ N.,				5	—	8·4	—	Position 49° 50′		
° 28′ W.			25	—	5·8	—	2° 30′ W.				25	—	8·0	—	2° 22′ W.		
unding 68 m.			50	10·9	3·1	7·8	Sounding 67 m.				50	11·4	10·0	1·4	Sounding 184		
			65	10·9	4·0	6·9					64	11·4	9·2	2·2			

Depth (m.)	Total-P (mg. P/m.^{3})	Phosphate-P (mg. P/m.^{3})	Difference
	4. x. 48		
0·5	11·4	5·4	6·0
5	12·8	5·8	7·0
15	10·8	6·0	4·8
25	11·7	7·2	4·5
50	12·8	8·7	4·1
70	12·3	8·0	4·3
	8. xi. 49		
0	18·0	10·3	7·7
10	13·9	10·0	3·9
25	13·3	10·5	2·8
50	13·3	10·5	2·8
70	14·3	10·4	3·9
	14. i. 49		
0	21·2	16·0	5·2
5	15·8	15·2	0·6
25	14·9	13·9	1·0
50	14·8	14·0	0·8
	13. x. 48		
5	—	8·4	—
25	9·9	7·6	2·3
50	8·6	7·6	1·0
75	11·5	7·6	3·9
100	10·3	7·8	2·5
150	11·2	7·3	3·9

Depth (m.)	Total-P (mg. P/m.^{3})	Phosphate-P (mg. P/m.^{3})	Difference
	27. x. 48		
0·5	10·5	8·8	1·7
5	12·4	8·6	3·8
25	12·9	9·3	3·6
50	11·0	8·6	2·4
70	12·1	9·6	2·5

THE BOTTOM FAUNA OF GREAT WEST BAY

By N. A. Holme, B.A.

Zoologist at the Plymouth Laboratory

(Text-fig. 1)

CONTENTS

	PAGE
Introduction	163
Methods	164
Great West Bay	165
Teignmouth Bay	165
Clean Sand	165
Mixed Grounds	168
Muddy Grounds	168
Torbay	172
Grounds off Berry Head	172
'The Corner'	172
Start Bay	176
Comparison with Ford's Survey	176
Comparison with the Plymouth Fauna	179
Note on *Crepidula fornicata*	180
Summary	181
References	181
Appendix	182

Introduction

At the end of the last century extensive investigations were made of the trawling grounds in the bay between Start Point and Portland, sometimes known as Great West Bay (see Stead, 1896; Holt, 1898; Garstang, 1903; Kyle, 1903; and Todd, 1903). Although these deal mainly with the food-fish of the area, Todd gives an account of invertebrates brought up in the trawl. Since the trawl mainly samples the 'epifauna' of the sea-bottom, no comparison will be made of Todd's results with those obtained in the grab surveys to be described.

In November 1923, Mr E. Ford made a survey of the bottom fauna of the Bay, using a $\frac{1}{10}$ m.^{2} Petersen grab. With the exception of a number of stations in Start Bay (see Ford, 1925), the results were not published. Mr Ford has kindly lent me the notes on his collections, some of which are included in this paper.

In the summer of 1948 a cruise was made in the western side of the Bay; samples being taken at thirty-seven stations with the bottom-sampler described by Holme (1949). At each station between one and five hauls were made, each covering an area of $\frac{1}{20}$ m.^{2}. The results are in the main very similar to those of Ford, showing that it is possible to make a reasonably reliable qualitative survey of a fairly large area using these methods. They also show that the bottom-fauna has not changed to any extent in the past 25 years.

The survey was made during the term of a D.S.I.R. research grant at the

Plymouth Laboratory. I am grateful to the Director and staff for facilities afforded during this period.

I am indebted to Captain C. A. Hoodless and the crew of R.V. *Sabella* for their assistance in taking the samples, and to Miss U. M. Grigg for help in sorting and preserving specimens during the cruise.

The following have kindly identified certain species: Miss S. M. Davies (*Eone*), Mr G. M. Spooner (Amphipoda), Miss U. M. Grigg (some of the Mollusca), Mr H. G. Vevers (Echinodermata). The author is responsible for the other identifications.

Methods

Except for a few dredge hauls, collections were made with the 'scoop-sampler', covering a nominal area of $\frac{1}{20}$ m.^{2}, and digging to a maximum depth of 15 cm. Many of the grounds are muddy and therefore fairly suitable for working with either the Petersen grab or the new sampler. Quantitative differences may be due either to changes in the density of the fauna over 25 years or to the relative efficiency of the two samplers.

On most grounds the scoop-sampler took a fairly adequate sample, but seldom came up full, the volume obtained corresponding to a 'bite' of depth 6–8 cm. It is unlikely that much soil was lost during hauling as all stations were worked in perfectly calm weather.

Positions were fixed by compass bearings on to the shore, which was in sight at all but one station. Station lists are given in Tables XI and XII (pp. 182–3). The writer's soundings have been reduced to chart datum.

Since tidal streams are weak the hauls at each station could be taken without the ship drifting more than perhaps 100 m., usually much less.

Collections at each station were put together and sieved through a mesh of 1, 2, or 3 mm., depending on the grade of soil. Smaller Crustacea and worms may have been lost when the larger-meshed sieves were employed. A soil sample from each station has been kept.

At certain stations, where the bulk of the sievings was great, only a proportion was kept for examination. To this was added any large or conspicuous animals seen in the rest of the sample. The numbers recorded at these stations are, therefore, not strictly quantitative, and can only be taken to represent the minimum numbers present in the sample. Owing to rather hasty preservation, inevitable when working through large quantities of material at sea, some of the smaller animals have not been identified further than the genus. Other specimens may, however, have been sufficiently well preserved to enable specific identification. Thus the recording of *Pectinaria koreni* and *Pectinaria* sp. from one station does not necessarilymean that more than one species was present.

Nomenclature usually follows the *Plymouth Marine Fauna* (Mar. Biol. Assoc., 1931).

Great West Bay

Great West Bay is 48 miles across from Start Point to Portland, and extends 20 miles inwards. Its area is about 650 square miles. The western side is sheltered from westerly winds by the coastline; this and the absence of Atlantic swell make the sea rather less rough than off Plymouth.

Tidal currents in the Bay are weaker than in the main English Channel, but reach over 2 knots (3·7 km./hr.) at Start Point and Portland Bill. Off Berry Head the current reaches only $\frac{3}{4}$ knot, while in Teignmouth Bay it is scarcely felt.

The bottom is variable, but coarse deposits are rare and localized. The most significant feature is the large amount of mud deposited, particularly off Berry Head and in Torbay. In parts of Start Bay and on 'the Corner', however, the soil is fairly clean, consisting of coarse sand or fine gravel.

The rivers Exe, Teign and Dart empty into the Bay, but do not affect the salinity outside their estuaries.

The area investigated will be considered under five headings: Teignmouth Bay, Torbay (worked only by Mr Ford), grounds off Berry Head, 'the Corner' fishing grounds, and Start Bay.

Teignmouth Bay

Teignmouth Bay extends from the Orestone to Straight Point, and has a maximum depth of *c.* 22 m. Over much of the bay the depth is about 20 m. The bay is exposed to the south and east, but sheltered from the north and west by the coastline.

Three fairly distinct types of bottom are found: clean sand; mixed grounds of sand, mud and gravel; and mud.

Clean Sand

This occurs in a belt parallel to the shore off Dawlish and Exmouth. Farther offshore the sand gives way to gravel deposits. The depth is less than 11 m. Towards Dawlish the sand is finer and slightly muddy.

In 1948 the following stations were worked in this area: 1, 2, 12 and 14–16 (Table I). The fauna off Exmouth (Stations 1 and 2) is poor, but becomes richer towards Dawlish.

Species characteristic of the area are: *Sigalion mathildae*, *Nephthys* sp., *Magelona papillicornis*, *Iphinoë trispinosa*, *Bathyporeia* spp., *Tellina fabula*, *Donax vittatus*, *? Spisula subtruncata* and *Ensis* sp.[1] *Echinocardium cordatum* is quite common at Station 16, but is rare or absent elsewhere.

Ford did not work this area.

[1] A note on the species of *Ensis* to be found in the area will be published shortly.

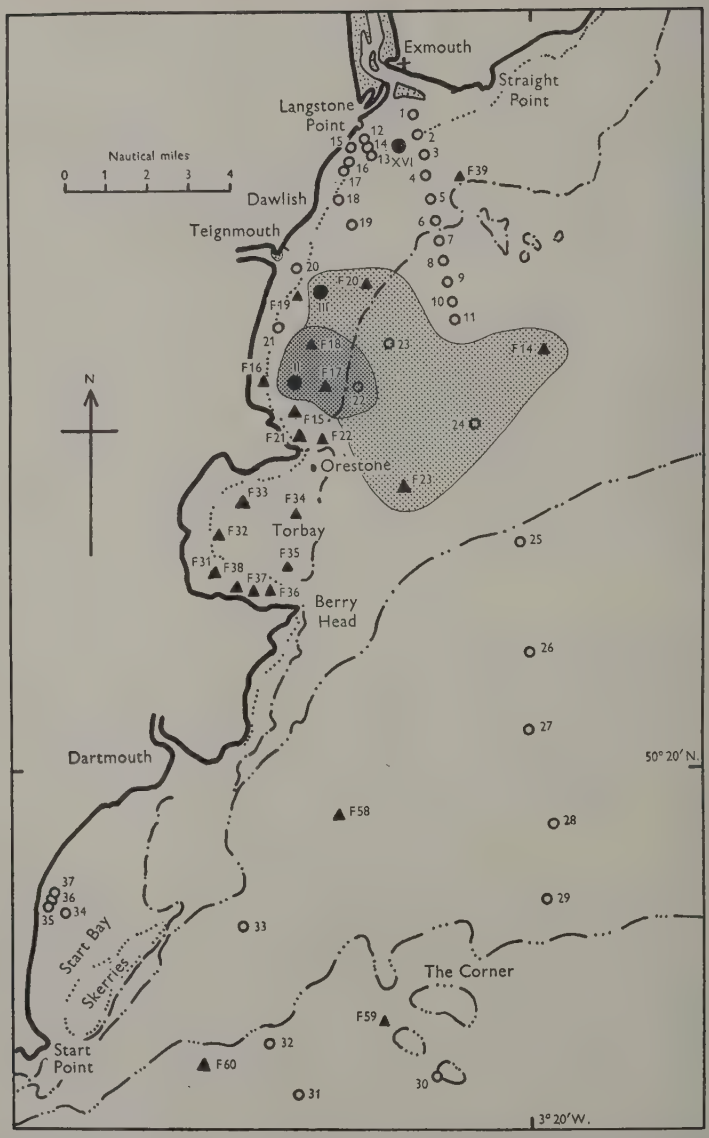

Fig. 1. Map of the western side of Great West Bay, showing stations worked by Mr Ford in 1923 and by the author in 1948. ▲, 1923 stations (Petersen grab); ○, 1948 stations (scoop-sampler); ●, 1948 dredge-hauls. ····, 5-fathom line; –·–, 10-fathom line; —·—, 20-fathom line; —···—, 30-fathom line. ▒, area occupied by living *Turritella*; ▒, area where dead *Turritella* shells are abundant.

Table I. Fauna of Fine Clean Sand in Teignmouth Bay

Notes on Stations

Station 1. 29. vii. 48. Exmouth Church, 349°, 1·2′. Clean sand.
Station 2. 29. vii. 48. Exmouth Church, 349°, 1·7′. Gravel and sand.
Station 12. 30. vii. 48. Langstone Point, 334°, 0·35′. Clean sand.
Station 14. 30. vii. 48. Langstone Point, 334°, 0·55′. Clean fine sand overlying gravel.
Station 15. 30. vii. 48. Langstone Point, 022°, 0·55′. Clean fine sand and some gravel. *Donax* picked out, and fauna sorted from two-thirds of total gravel.
Station 16. 30. vii. 48. Langstone Point, 013°, 0·9′. Sand.
The nominal area of each haul is 0·05 m.

Station	1	2	12	14	15	16
Depth (m.)	5·5	10·5	5·5	7·5	5	10·5
Area (m.²)	0·15	0·05	0·1	0·05	0·05	0·2
Sieve (mm.)	1	3	1	1	1	1
Coelenterata						
?*Peachia hastata*	..	..	..	..	..	3j.
?*Sagartia* sp.	..	..	..	..	..	1
Nemertini						
Nemertine sp.	..	..	1	..	..	..
Polychaeta						
Sigalion mathildae	..	..	2	..	..	*c.* 4
Sthenelais boa	..	..	..	..	..	1
Phyllodoce sp.	1	..	..	..	..	3
Nereis sp.	..	..	..	..	..	1
Nephthys sp.	*c.* 13	..	*c.* 3	..	..	4
Scoloplos armiger	..	..	..	..	..	1
Nerine sp.	..	..	..	..	..	1
Magelona papillicornis	*c.* 40	..	64	5	10	10
?*Owenia* tubes	..	..	..	..	..	3
Pectinaria koreni	?1	2	..	..	..	..
?*Lanice* tubes	..	1	..	..	..	6
Terebellid	..	1j.	..	..	..	..
Polychaeta indet.	1	1	3	..	1	1
Crustacea						
Iphinoë trispinosa	20	1	3	1	..	..
Diastylis laevis	2	..	..	..	..	1
Diastylis sp.	..	..	1	..	..	..
Pseudocuma cercaria	1	..	..	..	..	..
Ampelisca brevicornis	..	..	..	..	..	3
Bathyporeia guilliamsoniana	4	..	3	..	1	..
Bathyporeia elegans	..	..	3	..	?3	?1
Urothoë grimaldii	..	..	3	..	..	..
Leucothoë lilljeborgi	..	..	..	..	..	4
Nototropis swammerdami	1	..	..	..	..	..
Gammarus locusta	1	..	..	..	..	..
Amphipoda indet.	..	..	5	..	..	..
Prawn	..	1	..	..	..	..
Corystes cassivelaunus	..	..	..	..	..	1j.
Mollusca						
Nucula nitida	..	..	..	..	..	1
?*Pecten maximus*	1j.	..	..	..	..	..
Chlamys opercularis	1j.	..	..	..	..	..
Montacuta ferruginosa	..	..	..	..	..	2
Tellina fabula	2j.	..	1j.	..	..	2j.
Abra alba	..	..	..	..	..	1
Abra sp.	4j.	..	..	..	..	..
Donax vittatus	..	..	2j.	..	1	..
?*Spisula subtruncata*	6j.	..	..	..	..	1j.
Lutraria sp. (siphons)	..	..	..	..	..	2
Mysia undata	..	..	..	..	..	1
Chione striatula	..	..	..	..	..	1
?*Cardium aculeatum*	1j.	..	..	..	..	..
?*Cardium tuberculatum*	1j.	..	..	..	..	..
Ensis sp.	4j.	..	2	..	..	2
Lamellibranchs indet.	8	..	4j.	..	..	1
Philine aperta	..	..	1	..	..	1
Polyzoa						
Cellaria sp.	+	..	..	..	..	..
Echinodermata						
Acrocnida brachiata	..	..	..	..	..	2
Echinocardium cordatum	..	..	1j.	..	..	3
Labidoplax digitata	..	..	..	..	..	5

?, identity doubtful; j., small specimens; +, present, but numbers uncertain; ++, abundant.

Mixed Grounds

These occur off-shore in Teignmouth Bay in a depth of 10–23 m. Stations 3–11, 13 and 23 were worked in this area (Tables II and III). Deposits are of sand, fine shell fragments, and mud, sometimes mixed with fine gravel.

Characteristic species are: *Cerianthus lloydi*, *Melinna palmata*, *Phascolion strombi* (often in empty *Turritella* shells), *Eupagurus* spp., *Aloidis gibba*, *Cultellus pellucidus* and *Amphiura filiformis*.

Egg-clusters of *Turritella communis* were common at this time, and when trawling the meshes of the net came up covered with them. The presence of the Salcombe commensal, *Lepidasthenia argus*, at Station 3 is of interest. Although not taken in the grab hauls, *Gibbula magus* was found to be abundant off Langstone Point (dredge-haul XVI). A number of dredgings in the area showed that it was common only at this one station, where the bottom was of gravel.

Ford's Station 39, in this area, was evidently near a rocky ledge running southward from Straight Point. This is indicated by the presence of *Psammechinus miliaris* in the sample.

Muddy Grounds

These occur between Dawlish and the Orestone. Between Dawlish and Teignmouth the ground becomes progressively muddier, and north of the Orestone there is a deposit of mud in which *Turritella communis* is very abundant. The depth is between 10 and 22 m., and Stations 17–22 were worked in this area (Table IV).

Where living *Turritella* is abundant, only two or three other species are found. These include *Eupagarus bernhardus* which inhabits the empty shells. The estimated extent of the *Turritella* bed is shown in Fig. 1. At some stations living *Turritella* were abundant, at others large numbers of dead and worn shells were taken. In dredge-haul II living shells formed such a large proportion of the catch that they half-filled a galvanized iron bath. In dredge-haul III many white and dead shells were taken, but very few living ones occurred.

Mr Ford worked a number of stations in this bed, and the area shown on Fig. 1 is based on collections made on both cruises. There seems to be an area north of the Orestone where the animals live in abundance, from which dead shells are swept to the north and east by waves or currents.

It is of interest to note that Kyle (1903) records oysters (*Ostrea edulis*) from this area:

> 'From Hope's Nose to off Teignmouth there is a stretch of hard ground on which oysters are fairly abundant. As showing the trend of the currents in Teignmouth Bay, it may be mentioned that the empty shells congregate in masses behind the Orestone on the Torbay side.' (Hope's Nose is the headland opposite the Orestone).

Oyster shells are now rare or absent in Teignmouth Bay.

Table II. Fauna of Mixed Muddy and Gravel Grounds in Teignmouth Bay

Note. With most samples large animals were picked out, and a fraction of the sievings sorted (see p. 164). Numbers are those picked out, together with the subsample, which has not been multiplied by a factor.

Station 3. 29. vii. 48. Exmouth Church, 348°, 2·2′. Muddy sand and pebbles, overlying grey clay. One-quarter sorted.
Station 4. 29. vii. 48. Exmouth Church, 349°, 2·7′. Mud and a few pebbles. One-half sorted.
Station 5. 29. vii. 48. Exmouth Church, 349°, 3·3′. Fine shell fragments and sand. All sorted.
Station 6. 29. vii. 48. Exmouth Church, 349°, 3·8′. Muddy sand, gravel, and few shell fragments. Three-quarters sorted.
Station 7. 29. vii. 48. Exmouth Church, 349°, 4·3′. Fairly fine muddy sand. Small piece of red sandstone. One-quarter sorted.
Station 8. 29. vii. 48. Exmouth Church, 349°, 4·8′. Fairly fine muddy sand, with sandstone fragments. All sorted.

Station	3	4	5	6	7	8
Depth (m.)	14	17·5	19	19	20·5	21·5
Area (m.²)	0·15	0·1	0·1	0·15	0·1	0·15
Sieve (mm.)	3	3	3	3	3	3
Coelenterata						
Hydroid	..	..	..	+	..	..
Cerianthus lloydi	1	2	..	..	4	2
?*Peachia hastata*	1j.	..	..	..	..	..
Porifera						
Sponge	..	..	..	..	..	1
Polychaeta						
Lepidasthenia argus	1	..	..	..	..	..
Sthenelais boa	1	..	..	..	..	..
?*Glycera convoluta*	..	..	..	3	..	2
Glycera sp.	..	1	..	..	..	..
Nematonereis unicornis	1	..	1	1	..	..
Lumbriconereis sp.	..	..	..	1	..	1
Staurocephalus sp.	..	..	..	1	..	..
Stylaroides eruca	1	..	..	..	..	..
Scalibregma inflatum	..	..	1	..	..	..
?*Owenia* tubes	..	1	1	..	..	..
Pectinaria koreni	..	..	..	..	..	1
Pectinaria auricoma	..	..	1	..	..	..
Melinna palmata	2	16	4	6	..	1
Terebellid	..	..	1j.	..	..	..
Polychaeta	..	5	1	2	..	1
Gephyrea						
Phascolosoma elongatum	2	..	..	..	..	..
Phascolosoma vulgare	..	3	..	..	..	..
Phascolion strombi	..	..	1	3	..	..
Crustacea						
Amphipoda indet.	..	..	1	1	..	..
Eupagurus cuanensis	..	..	..	..	1j.	..
Gonoplax rhomboides	..	..	1j.	..	..	..
Mollusca						
Abra alba	..	..	1	..	..	..
Lutraria lutraria	..	..	..	1j.	..	..
Chione fasciata	..	..	..	..	1	..
Cardium ovale	..	..	..	..	..	1
Aloidis gibba	..	1	..	2	..	..
Cultellus pellucidus	..	..	..	..	..	1
Turritella communis	4	+*	1	..	..	1
Aporrhais pes-pelicani	..	..	..	..	..	2
Philine aperta	1	..	..	..	..	..
Polyzoa						
Cellaria sp.	..	..	1	..	+	1
Echinodermata						
Amphiura filiformis	..	..	..	1	?1	2
Cucumaria elongata	..	..	..	..	..	1

* One egg-cluster of *Turritella*.

For abbreviations, see Table I.

Table III. Fauna of Mixed Muddy and Gravel Grounds in Teignmouth Bay (continued)

Note

Station 9. 29. vii. 48. Exmouth Church, 349°, 5·3′. Coarse muddy sand and a few shell fragments. All sorted.
Station 10. 29. vii. 48. Exmouth Church, 349°, 5·8′. Soil as at Station 9. One-tenth sorted.
Station 11. 29. vii. 48. Exmouth Church, 349°, 6·2′. Soil as at Stations 9 and 10. All sorted.
Station 13. 30. vii. 48. Langstone Point, 334°, 0·75′. Gravel and muddy sand. One-tenth sorted.
Station 23. 30. vii. 48. Orestone, 222°, 3·5′. Muddy sand with *Turritella* shells. All sorted.

Station	9	10	11	13	23
Depth (m.)	22	21·5	22	10·5	23
Area (m.²)	0·2	0·25	0·1	0·1	0·1
Sieve (mm.)	3	3	3	3	1
Coelenterata					
Cerianthus lloydi	2	1	..	..	..
?*Peachia hastata*	..	..	..	1 j.	..
Porifera					
Sponge	..	..	..	..	2*
Nemertini					
Nemertine sp.	1	..	..	..	..
Polychaeta					
Phyllodoce sp.	1	..	..	..	..
Nereis longissima	..	..	..	..	1
Nephthys sp.	1	2	2	1	2
Hyalinoecia bilineata	..	1	..	..	..
?*Spiophanes bombyx*	..	..	..	..	2
?*Owenia* tubes	4	5	1	..	..
Pallasia murata	..	1	..	..	..
Melinna palmata	5	10	1	4	..
?*Lanice* tubes	1	..	..	..	..
Polychaeta indet.	10	6	*c.* 8	2	..
Gephyrea					
Phascolosoma vulgare	..	1	..	..	..
Phascolion strombi	..	1	2	..	11
Crustacea					
Coremapus versiculatus	..	..	..	..	1
Amphipoda indet.	..	..	1	..	..
Eupagurus bernhardus	..	1	..	..	..
Eupagurus cuanensis	..	1	..	..	..
Eupagurus sp.	..	..	..	..	1 j.
Mollusca					
Nucula radiata	..	1	..	..	..
Nucula nitida	..	1	..	..	..
Abra alba	..	..	1	..	3
Abra nitida	..	..	3	..	..
Abra sp.	..	3	..	..	..
Spisula subtruncata	..	1	..	..	..
Lutraria sp. (siphons)	..	..	1	..	..
Dosinia lupinus	2	..	..	..	..
Aloidis gibba	1	1	..	..	..
Cultellus pellucidus	1	7	3	..	..
Turritella communis	..	..	1	..	1†
Nudibranch	1	..	..	..	..
Polyzoa					
Cellaria sp.	1	..	1	..	1
Echinodermata					
Ophiothrix fragilis	4	1	..	..	..
Amphiura filiformis	..	1	..	..	..
Thyone roscovita	2	..	..	..	..
Labidoplax digitata	3	2	..	..	..

* Attached to *Turritella* shells. † Also *c.* 250 dead worn shells.
For abbreviations, see Table I.

Table IV. Fauna of Muddy Grounds in Teignmouth Bay

Note

Station 17. 30. vii. 48. Langstone Point, 017°, 1·15′. Fine slightly muddy sand, and some gravel. Sampler not digging deeply.
Station 18. 30. vii. 48. Teignmouth Pier, 229°, 1·7′. Fine muddy sand, overlying gravel. Large animals picked out, and half the sieved gravel examined.
Station 19. 30. vii. 48. Teignmouth Pier, 251°, 1·7′. Gravel and sand in first two hauls, last three of sand. Large animals picked out, and one-fifth of gravel examined.
Station 20. 30. vii. 48. Teignmouth Pier, 324°, 0·6′. Fine sand with little mud.
Station 21. 30. vii. 48. Teignmouth Pier, 004°, 1·9′. Very fine muddy sand.
Station 22. 30. vii. 48. Orestone, 210°, 2·2′. Mud, with old *Turritella* shells.

Station	17	18	19	20	21	22
Depth (m.)	10·5	12·5	16·5	9·5	10·5	21·5
Area (m.²)	0·2	0·1	0·25	0·1	0·15	0·1
Sieve (mm.)	1	1	1	1	1	1
Coelenterata						
Cerianthus lloydi	..	..	3	..	..	..
?*Peachia hastata*	1	..	..	..	..	..
Anemone	..	..	..	..	1	..
Polychaeta						
Aphroditidae (mainly polynoids)	1	..	1	..	1 j.	..
Sigalion mathildae	1	..	1	2	..	..
Sthenelais boa	..	..	..	..	1	..
Phyllodoce sp.	..	..	..	..	1	..
?*Eteone* sp.	1	..	..	..	..	..
Nereis longissima	..	..	..	..	..	1 j.
Nereid	..	..	1 j.	..		..
Nephthys sp.	6	..	2	..	*c.* 6	..
Glycera sp.	..	..	1	..	..	
Eone nordmanni	..	1	1	..	?1	..
Nematonereis unicornis	..	..	1	..	..	..
Lumbriconereis sp.	1	..	1	..	..	..
Spionid	..	..	1	1	..	..
Spiophanes bombyx	..	..	...	..	*c.* 10	..
Magelona papillicornis	17	..	2	2	1	..
Notomastus latericeus	..	..	..	..	..	2 j.
?*Owenia* tubes	2	..	2	2	..	..
Pallasia murata	..	..	+*	..	..	..
Pectinaria sp.	..	1	..	..	..	..
Melinna palmata	3	..	12	1	*c.* 25	..
Amphitrite edwardsi	1 j.	..	..	..	..	..
Lanice tubes	..	..	..	3	..	..
Polychaeta indet.	18	5	7	1	*c.* 20	..
Gephyrea						
Phascolion strombi	..	1	..	..	..	..
Crustacea						
Iphinoë trispinosa	..	..	..	..	2	..
Diastylis laevis	..	..	..	..	1	..
Ampelisca brevicornis	..	..	..	..	3	..
Ampelisca tenuicornis	..	..	1	..	..	..
Bathyporeia sp.	..	..	..	..	2	..
Urothoë grimaldii	..	..	..	..	2	..
Amphipoda indet.	..	..	..	2	..	..
Eupagurus bernhardus	1 j.	..	..	..	..	1 j.
Mollusca						
Nucula nitida	..	..	..	2 j.	..	..
Thyasira flexuosa	..	..	..	..	3	..
Montacuta ferruginosa	1	..	..	..	..	..
Tellina fabula	8	..	..	..	5	..
Abra alba	..	..	..	..	7	..
Abra sp.	..	..	..	1	..	..
Spisula subtruncata	..	..	..	..	1	..
Lutraria sp. (siphons)	2	..	1	..	1	..
Mysia undata	..	..	1 j.	..	..	..
Chione striatula	1 j.	..	..	1 j.	..	..
?*Mya truncata*	..	..	1 j.	..	..	..
Ensis sp.	1 j.	..	4	..	..	..
Cultellus pellucidus	1 j.	..	..	..	..	..
Lamellibranch indet.	..	..	..	..	1 j.	..
Gibbula magus	..	2	..	..	..	..
Turritella communis	10	1	..	..	1	50†
Retusa sp.	..	..	..	..	1	..
Philine aperta	..	..	..	..	2	..
Echinodermata						
Amphiura filiformis	1	1	7	1	2	..
Echinocardium cordatum	1	..	..	..	..	..
Cucumaria elongata	..	..	..	..	1	..
Leptosynapta inhaerens	1	..	1	..	..	..
Labidoplax digitata	1	..	..	..	..	..

* Piece of tube. † *c.* 2300 worn old shells.
For abbreviations, see Table I.

Outside the *Turritella* bed characteristic species are: *Sigalion mathildae*, *Melinna palmata*, *Lutraria* sp., *Chione striatula*, *Ensis* sp., *Turritella communis* and *Amphiura filiformis*.

Siphons of large specimens of *Lutraria* sp., probably *L. lutraria*, were taken at a number of stations. This mollusc digs to a considerable depth and the shell is out of reach of the 'bite' of the sampler.

Torbay

Torbay was worked by Ford in 1923, but was not visited in 1948. Stations F31–38 (Table V) were worked, in a depth of 11–16 m. Torbay is sheltered on three sides, being open only to the eastward. The bottom is mostly fine muddy sand, and the fauna is rather similar to that off Teignmouth.

The main features are the presence of large numbers of *Nucula nitida* and *Lutraria lutraria* (?), the siphons only of the latter being taken in the Petersen grab. Ford notes that *Echinocardium* was more in evidence here than elsewhere in the Great West Bay.

Other typical species are: *Nephthys* sp., *Melinna* sp., *Ampelisca* sp., *Thyasira flexuosa*, *Abra alba*, *Cultellus pellucidus* and *Amphiura filiformis*.

Grounds off Berry Head

Off Berry Head there is a deposit of very fine sand and mud. Stations 24–27 (Table VI) were worked about 6 miles from shore, in a depth increasing from 30 to 51 m. The soil is similar at all stations except 27, where it is rather coarser.

Characteristic species are: *Nephthys* sp., *Lumbriconereis* sp., *Notomastus latericeus*, *Pectinaria koreni*, *Callianassa subterranea*, ?*Abra alba*, *Chione striatula*, *Cultellus pellucidus*, *Turritella communis* (in small numbers), *Amphiura filiformis*, and *Leptosynapta inhaerens*. *Callianassa* occurs at all stations from 25 to 29, and evidently forms a bed of considerable density in this area. The average density is 13 per m.^{2}

'The Corner'

South of Station 27 the bottom becomes coarser and less muddy. Several species seem to reach a larger size than at previous stations. The area is trawled by Brixham fishing vessels, but is not very productive.

Stations 28–33 were worked in this area in a depth of 51–60 m. (Table VII). The bottom is of coarse slightly muddy sand, characteristic species being: hydroids, *Pectinaria koreni*, *Nucula nitida*, *Amphiura filiformis* and *Echinocyamus pusillus*.

Echinocyamus appears for the first time at Station 28, not having been taken at previous stations. Station 33 has a bottom of finer sand with a fauna similar to that found on similar soils in Teignmouth Bay.

TABLE V. FAUNA OF TORBAY. SAMPLED BY MR FORD IN 1923 WITH TWO HAULS OF THE $\frac{1}{10}$ M.^{2} PETERSEN GRAB AT EACH STATION

Note

Station F 31. 15. xi. 23. Saltern Cavern NW, Churston Point, SW by W½W. Sand.
Station F 32. 15. xi. 23. Red Cliff Hotel NW by N; Roundham Head NW by W½W. Silty sand.
Station F 33. 15. xi. 23. Orestone E by N; Torquay Pier N by W. Muddy sand.
Station F 34. 15. xi. 23. Orestone NE by N; Thatcher Rock N. Mud and sand.
Station F 35. 15. xi. 23. Berry Head S; Brixham Breakwater Light SW by W. Mud and sand.
Station F 36. 15. xi. 23. Berry Head SE; Brixham Breakwater Light WSW. Sand harder and cleaner than at Station 35.
Station F 37. 15. xi. 23. Old Battery SW; Brixham Breakwater Light SE by E. Sandy mud.
Station F 38. 15. xi. 23. Quarries WNW; Fishcombe Point S½E. Mud, with some *Zostera*.

Station	F31	F32	F33	F34	F35	F36	F37	F38
Sounding (m.) ..	11	15	14	16	15	12	12	?
COELENTERATA								
Anemone	..	..	..	..	..	..	1	..
PLATYHELMINTHES								
Polyclad sp.	..	..	..	..	..	..	..	1
NEMERTINI								
Nemertine sp.	..	1	1	..	1	..	..	..
POLYCHAETA								
Sigalion sp.	..	..	..	..	..	..	1	..
Sthenelais limicola	..	1	..	..	..	..	1	2
Phyllodoce maculata	..	..	..	..	1	..	..	..
Nereis sp.	..	1	..	..	..	..	..	..
Nephthys sp.	6	10	8	6	8	7	7	9
Ammotrypane sp.	..	1	..	..	..	..	1	..
Scalibregma sp.	..	..	..	..	..	..	..	1
Notomastus latericeus	..	1	..	..	..	..	..	..
Pectinaria auricoma	..	1	..	..	..	..	..	..
Melinna sp.	+	5	3	2	..	..	+	+
Lanice conchilega tubes	3	..	1	..	..	6	..	2
Polychaeta indet.	+	+	+	6	+	..	+	+
CRUSTACEA								
Diastylis sp.	..	2	1	..	..	..	..	..
Ampelisca sp.	6	1	3	4	..	..	2	1
?*Maera* sp.	1	..	..	..	..	..	..	..
Amphipoda indet.	..	..	..	..	..	..	1 j.	..
Caprellid	..	..	..	..	..	..	..	1
Porcellana longicornis	1	..	..	..	..	..	..	..
Macropodia sp.	..	..	..	..	..	..	..	2 j.
MOLLUSCA								
Nucula nitida	7	25	9	12	2	3	4	22
Thyasira flexuosa	..	6	1	..	..	..	1	5
Mysella bidentata	..	3	..	..	..	1	..	2
Montacuta ferruginosa	..	..	..	..	4	..	..	..
Tellina fabula	5	3	..	1	..	..	..	6
Abra alba	..	..	3 j.	4 j.	29	..	1	6 j.
Abra sp.	..	7 j.	..	..	..	..	..	..
Mactra corallina	1 j.	..	..	..	..	..	..	..
?*Spisula elliptica*	..	..	..	1 j.	..	..	..	..
?*Lutraria lutraria* (siphons)	..	1	..	..	25*	1	..	..
Chione striatula	..	1	..	2	..	..	2	..
Cardium echinatum	..	..	..	..	2	..	..	..
Aloidis gibba	..	..	..	..	..	..	1 j.	..
Cultellus pellucidus	1	1	..	9	..	..	..	2
Philine sp.	..	5 j.	..	1	..	..	..	4 j.
ECHINODERMATA								
Astropecten sp.	..	..	..	..	1	..	..	..
Amphiura filiformis	1	13	+	..	7	..	..	..
Ophiuroid	1	..	..	2	..	..	1 j.	..
Echinocardium cordatum	..	1	1	..	13 j.	..	..	..

* In all but four specimens siphons only were taken.
For abbreviations, see Table I.

Table VI. Fauna of Grounds off Berry Head. Soil: Fine Sand and Mud at all Stations

Note

Station 24. 4. viii. 48. Berry Head, 225°, 6·2′.
Station 25. 4. viii. 48. Berry Head, 254°, 5·7′.
Station 26. 4. viii. 48. Berry Head, 280°, 5·8′.
Station 27. 4. viii. 48. Berry Head, 297°, 6·4′.

Station	24	25	26	27
Depth (m.)	30·5	40·5	48	51
Area (m.²)	0·1	0·1	0·15	0·25
Sieve (mm.)	1	1	11	1
Coelenterata				
Hydroids	..	..	+	+
?*Sagartia* sp.	9	..	..	1
Nemertinea				
Nemertine sp.	..	1	13	2
Polychaeta				
Aphroditidae	..	..	1	1
?*Harmothoë lunulata*	..	..	1	..
Phyllodoce sp.	..	1	1	..
Nephthys sp.	..	3	6	*c.* 3
Glycera convoluta	..	..	..	3
Glycera sp.	..	..	1 j.	..
?*Eone* sp.	..	1	1	..
Lumbriconereis sp.	1	..	2	2
Scoloplos armiger	..	1	2	..
Spiophanes bombyx	1	..	?2	..
Cirratulid	..	2	6	..
?*Stylaroides flabellata*	..	..	2	..
Scalibregma inflatum	1	..	..	..
Scalibregma sp.	..	..	..	1
Notomastus latericeus	3	10	3	1
?*Owenia* tubes	..	..	..	2
Pectinaria koreni	1	..	4	22
Terebellid	..	?3 j.	..	1
Polychaeta indet.	..	11	7	4
Crustacea				
Diastylis sp.	..	..	..	1
Cumacean	..	..	1	..
Ampelisca tenuicornis	1	1	1	..
Harpinia antennaria	..	..	2	..
Callianassa subterranea	..	2	2+4 j.	2 j.
Decapoda	..	..	2	..
Mollusca				
Mysella bidentata	..	..	..	5
?*Abra alba*	..	10 j.	4 j.	27 j.
?*Dosinia exoleta*	..	..	..	1
?*Dosinia lupinus*	..	..	..	1 j.
Chione striatula	..	..	3 j.	1+6 j.
?*Cardium aculeatum*	..	..	..	1 j.
Aloidis gibba	..	..	3 j.	..
Cultellus pellucidus	1 j.	1 j.	..	1+24 j.
Psammosolen chamasolen	..	..	1	..
Lamellibranch indet.	..	..	1	..
Turritella communis	12*	+†	+†	..
Retusa sp.	..	1	..	..
Echinodermata				
Amphiura filiformis	..	..	10 j.	51
Echinocardium cordatum	..	..	..	2
Leptosynapta inhaerens	..	..	1	12

* Also two egg-clusters. † One egg-cluster only.
For abbreviations, see Table I.

Table VII. Fauna of 'The Corner' Region

Note

Station 28. 4. viii. 48. Berry Head, 310°, 8·2′. Muddy sand with shell fragments. Soil coarser and less muddy than at Station 27.
Station 29. 4. viii. 48. Berry Head, 319°, 9·4′. Coarse slightly muddy sand. One-quarter sorted after picking out large animals.
Station 30. 4. viii. 48. Start Point, 275°, 9·6′. Coarse slightly muddy sand, and shell fragments. Sampler not bringing up much soil.
Station 31. 4. viii. 48. Start Point, 282°, 6·3′. Coarse slightly muddy sand. One-quarter sorted.
Station 32. 4. viii. 48. Start Point, 270°, 5·4′. Coarse slightly muddy sand. One-quarter sorted.
Station 33. 4. viii. 48. Start Point, 240°, 5·6′. Slightly muddy sand.

Station	28	29	30	31	32	33
Depth (m.)	51	54·5	60	59·5	58·5	49
Area (m.²)	0·25	0·15	0·1	0·1	0·15	0·2
Sieve (mm.)	2	2	1	1	2	?
Coelenterata						
Hydroids	1	1	+	..	++	..
Cerianthus lloydi	..	..	..	..	4	..
Nemertinea						
Nemertine	..	2	..	..	..	..
Polychaeta						
Aphroditidae	..	1	..	..	..	1
Sigalion mathildae	..	..	..	..	..	1
Sthenelais limicola	..	..	..	..	..	1
Phyllodocidae	..	..	..	..	..	1
Nereidae	..	..	..	..	1 j.	..
Nephthys sp.	*c.* 3	..	..	..	..	*c.* 6
Glycera convoluta	..	1	1	..	..	..
Glycera sp.	..	..	..	..	..	3
Eunicidae	1	..	..	..	..	..
Lumbriconereis sp.	..	2	1	..	..	5
Magelona papillicornis	..	..	1	..	..	160
Scalibregma inflatum	..	..	..	..	..	1
?*Owenia* tubes	*c.* 3	2	1	..	1	..
Pallasia murata	1	..	..	..	..	..
Pectinaria koreni	10	4	..	1	1	13
Pectinaria auricoma	1	..	..	..	..	..
?*Lanice* tubes	..	4	..	..	1	..
Dasychone bombyx	..	..	..	..	1	..
Terebellid	..	1	1	..	..	..
Polychaeta indet.	10	6	2	4	..	*c.* 20
Crustacea						
Ampelisca spinipes	..	..	..	1	..	..
Caprellid	..	..	..	..	1	..
Callianassa subterranea	1	1 j.	..	..	..	..
Upogebia stellata	..	..	..	1	..	..
Corystes cassivelaunus	1	..	..	..	..	2
Mollusca						
Chiton	..	..	..	..	1	..
Nucula nitida	1	1	1 j.	..	..	4
Diplodonta rotundata	..	..	..	1	..	..
Tellina donacina	..	..	..	1	..	..
Abra alba	..	..	..	..	10	15
?*Abra nitida*	2	2	..	..	..	..
Abra sp.	..	..	1	..	..	..
Gari ferroensis	1	..	..	..	..	..
Dosinia lupinus	1	1	..	..	..	..
Chione striatula	2	..	..	..	..	1
Cardium sp.	..	..	..	..	..	1 j.
Aloidis gibba	..	1	..	..	..	..
Ensis sp.	..	..	..	..	..	1 j.
Cultellus pellucidus	3	..	..	..	1	3 j.
Lamellibranch indet.	..	..	..	..	..	1
Dentalium sp.	..	..	..	1	..	..
Turritella communis	..	..	..	..	..	+†
Echinodermata						
Amphiura filiformis	33	7	..	1	3	6
Ophiura texturata	..	..	..	..	..	1
Echinocyamus pusillus	+*	+*	+*	+*	4*	..

* Empty tests of *Echinocyamus* common. † One egg-cluster.
For abbreviations, see Table I.

Start Bay

A mile or so off Slapton the bottom is of fine muddy sand, with the following fauna:

Station 34, 5 viii. 48. Start Point 128°, 3·2′. Fine slightly muddy sand. Depth 18 m. 0·1 m.² sampled. Sieve: 1 mm.

Phyllodocidae	1	?*Mysella bidentata*	2
Mageloma papillicornis	1	*Montacuta ferruginosa*	1
Polychaeta indet.	13	*Ensis* sp.	1
Nucula nitida	3	*Cultellus pellucidus*	2
Abra alba	9	*Natica catena*	1

Closer in-shore a gravel bottom occurs, with *Spisula solida* as the main inhabitant. This ground has already been described by Ford (1925), who found that the bed of *Spisula* extended for about 4 miles along the coast, in a depth of about 10 m. The density exceeded 1000 per m.² in six out of nine stations. In 1948 Stations 35–37 were worked on the *Spisula* bed. The results may be summarized thus:

Station 35	0·1 m.² sampled	Empty *Spisula* shells only
Station 36	0·15 m.² sampled	*Spisula solida* 58
		Chione fasciata 1
Station 37	0·05 m.² sampled	Empty *Spisula* shells only

Bearings and distances from Start Point were:

35: 181°, 3·3′; 36: 181°, 3·5′; 37: 182°, 3·7′.

Dredge hauls confirmed the abundance of *Spisula*, although it may be noted that the density recorded, 387 per m.², is considerably less than all but one (no. 50) of the nine stations sampled by Ford.

Comparison with Ford's Survey

The results of Ford's survey are given in Tables V, VIII, IX and X. From these it is clear that no major qualitative changes have occurred in the fauna. For example, the following were found in both surveys:

(1) The *Turritella* ground in Teignmouth Bay.

(2) The *Spisula* bed in Start Bay.

(3) A fauna with *Nephthys* sp., *Notomastus latericeus*, *Melinna palmata*, *Nucula nitida*, *Lutraria* sp., *Cultellus pellucidus* and *Amphiura filiformis* among the most abundant or widely distributed species.

Owing to the different types of sampler used and to the fact that the same stations were not revisited, a quantitative comparison of the fauna at the two different times is not possible. The *Spisula* bed may have declined in numbers, as shown above, and certain species, *Abra alba* for example, seem to have decreased in density. On the whole, however, there is no evidence of any overall change in the abundance of the fauna.

TABLE VIII. SAMPLES TAKEN BY MR FORD IN THE *TURRITELLA* BED IN TEIGNMOUTH BAY. TWO HAULS OF $\frac{1}{10}$ M.^{2} PETERSEN GRAB AT EACH STATION

Note

Station F 14. 13. xi. 23. Hope Nose W½S, The Ness NW by W. Mud and *Turritella* shells. Sample with over 700 dead and worn *Turritella* shells.

Station F 17. 13. xi. 23. Orestone S½W, Babbacombe Point W by S½S. Black mud and brownish sand. Ten empty *Turritella* shells taken.

Station F 18. 13. xi. 23. Babbacombe Point SW½S, The Ness N½E. Dark sand and mud. Thirty empty shells of *Turritella*, but these were fresh and pink in colour.

Station F 20. 13. xi. 23. Orestone S by W, The Ness NW. Muddy shell gravel with *Turritella* shells. Over 600 dead and worn shells taken.

Station F 23. 14. xi. 23. Orestone NW by W½W, The Ness N by W½W. Dark sandy mud and *Turritella* shells. Over 1200 white empty shells taken, but these were not badly worn.

Station	F14	F17	F18	F20	F23
Sounding (m.) ..	30	19	17	21	32
COELENTERATA					
Hydroid	1	..	..	..	..
Anemone	1	1	..	..	2
PLATYHELMINTHES					
Cryptocoelis sp.	1	..	..	..	..
POLYCHAETA					
Aphrodite sp.	..	..	..	1	..
Aphroditidae	1	..	..	..	..
Sthenelais sp.	1	..	..	..	..
Nephthys sp.	3	22	2	2	4
Goniada maculata	..	1	..	..	..
Scalibregma sp.	..	..	..	1	..
Ammotrypane sp.	..	..	1	..	..
Notomastus sp.	+	+	..	..	..
Owenia fusiformis	..	1	..	10	..
Melinna sp.	..	+	4	13	5
Lanice sp.	..	..	..	1	..
Terebellid	..	1	..	..	..
Sabellid	..	..	..	1	..
Polychaeta indet.	1	+	..	+	+
GEPHYREA					
Phascolion strombi	+	..	9	..	+
CRUSTACEA					
Ampelisca sp.	1	1	..	3	..
Amphipoda indet.	1	..	..	1	..
Shrimp	..	1	..	..	..
Eupagurus sp.	7 j.	..	..	6	..
Nika edulis	..	1	..	..	..
Gonoplax rhomboides	..	..	..	..	1
Porcellana longicornis	8	..	..	1	..
MOLLUSCA					
Thyasira flexuosa	1	3	..	3	..
Abra alba	?25	2 j.	..	7	..
Mactra corallina	..	1 j.	..	..	..
Aloidis gibba	..	..	..	1	..
Cultellus pellucidus	..	..	..	1	..
Bullinella cylindracea	..	..	1	..	..
Nassa reticulata	..	..	1	..	..
Turritella communis	58	..	70	..	38
ECHINODERMATA					
Ophiuroid	..	1 j.	..	..	..

For abbreviations, see Table I.

Table IX. Samples taken by Mr Ford on Various Grounds in Teignmouth Bay. Two Hauls of the $\frac{1}{10}$ m.^{2} Petersen Grab at Each Station

Note

Station F15. 13. xi. 23. Hope Nose S, Babbacombe Point W by S. Dark mud and sand.
Station F16. 13. xi. 23. Babbacombe Point S, Petit Tor NW. Fine red sand.
Station F19. 13. xi. 23. Hope Nose S by W, The Ness N. Fine red sand.
Station F21. 13. xi. 23. Black Head SW, Babbacombe NW by W. Very fine reddish sand.
Station F22. 13. xi. 23. Flat Rock SW$\frac{1}{2}$W, Black Head NW$\frac{1}{4}$W. Coarse muddy shale (unsuitable for grab work).
Station F39. 16. xi. 23. Clerk Point W by N, Straight Pt. N by E. Coarse muddy gravel.

Station	F15	F16	F19	F21	F22	F39
Sounding (m.) ..	15	10	10	14	22	22
COELENTERATA						
Hydroid	..	..	..	..	..	+
POLYCHAETA						
Aphroditidae	..	..	..	..	..	1
?*Sigalion* sp.	..	1	..	..	..	..
Sthenelais boa	..	..	..	..	..	1
Phyllodoce maculata	..	..	..	..	..	1
Nereis sp.	..	..	..	..	1	..
Nephthys sp.	7	1	6	10	1	1
Glycera sp.	..	..	..	..	1	6
Magelona sp.	..	..	..	..	..	1
Scalibregma sp.	..	..	..	..	2	8
Ammotrypane sp.	1	..	..	..	..	..
Notomastus sp.	..	..	..	+	+	..
Owenia fusiformis	5	..	16	1	5	..
Amphicteis sp.	..	1	..	..	..	..
Melinna palmata	++	..	..	*c.* 9	2	+
Amphitrite sp.	..	..	..	..	..	1
Lanice conchilega	*c.* 10	..	16	48	..	..
Terebellid	..	..	..	1	..	..
Polychaeta indet.	+	+	..	+	..	3
GEPHYREA						
Phascolosoma sp.	..	..	..	..	4	..
Phascolion strombi	..	..	..	..	..	2
CRUSTACEA						
Ampelisca sp.	9	..	..	8	..	6
Bathyporeia sp.	..	..	2	..	..	..
?*Hippomedon* sp.	1	..	..	..	..	..
Eupagurus sp.	..	..	..	..	..	1
Nika edulis	..	..	..	1	..	..
Portunus sp.	..	..	..	..	..	1 j.
MOLLUSCA						
Nucula nitida	4	1	..	7	1	..
Thyasira flexuosa	6	..	..	1	1	1
Diplodonta rotundata	..	..	..	..	..	1
Mysella bidentata	2	..	..	..	..	..
Tellina fabula	..	1	..	1	..	..
Abra alba	3 j.	2 j.	..	7 j.	2 j.	..
Abra nitida	2	..	..	..	..	..
Donax vittatus	..	..	1	..	..	..
Spisula sp.	..	1 j.	..	..	..	..
Lutraria lutraria (siphons)	..	4	..	..	..	..
Chione striatula	1	..	..	..	..	..
Aloidis gibba	..	1 j.	..	..	..	..
Ensis sp.	..	1 j.	..	..	..	..
Cultellus pellucidus	3	..	..	2	..	..
Turritella communis	..	..	..	..	..	1
ECHINODERMATA						
Amphiura filiformis	4	..	..	1	..	3
Psammechinus miliaris	..	..	..	..	..	1
Echinocardium cordatum	..	1	..	..	..	..
Cucumaria elongata	..	..	..	..	..	2
Synapta sp.	1	..	..	..	..	..

For abbreviations, see Table I.

TABLE X. SAMPLES TAKEN BY MR FORD IN THE 'CORNER' REGION. TWO HAULS OF $\frac{1}{10}$ M.^{2} PETERSEN GRAB AT EACH STATION

Note

Station F58. 20. xi. 23. Berry Head N 5 miles. Fine sandy mud.
Station F59. 20. xi. 23. Berry Head N 10 miles. Silty sand, gravel, and shells.
Station F60. 20. xi. 23. Start Point W by N$\frac{3}{4}$N, Downend Beacon N by E$\frac{3}{4}$E. Silty sand, gravel, and shells.

Station	F58	F59	F60
Sounding (m.)	48	59	57
COELENTERATA			
Hydroid	..	..	+
NEMERTINI			
Nemertine sp.	1	..	..
POLYCHAETA			
Sthenelais limicola	..	1	..
Sthenelais sp.	3	..	..
Ophiodromus flexuosus	1	..	..
Nephthys sp.	3	1	2
Phyllochaetopterus sp.	..	..	+
Chlorhaemid	1	2	..
Notomastus sp.	2	..	..
Owenia fusiformis	..	..	1
Maldanid	..	1	..
Lanice sp.	..	*c.*5	..
Polychaeta indet.	+	+	2
CRUSTACEA			
Ampelisca sp.	..	1	2
Palaemonid	..	..	1
Portunus sp.	..	1 j.	..
Gonoplax rhomboides	2	..	..
Ebalia sp.	..	..	1
Macropodia sp.	..	1 j.	..
MOLLUSCA			
Nucula nitida	..	1	..
Thyasira flexuosa	1	..	..
Tellina donacina	..	1	2
Abra alba	..	4	..
?*Abra nitida*	2 j.	..	..
Chione striatula	..	1	..
Cultellus pellucidus	4	2	..
Turritella communis	..	1	..
ECHINODERMATA			
Amphiura filiformis	..	1	..
Ophiuroid	..	..	1
Echinocardium cordatum	1	..	..

For abbreviations, see Table I.

COMPARISON WITH THE PLYMOUTH FAUNA

Ford (1923) has outlined the communities to be found on the level sea bottom at Plymouth; he found that the main communities represented were *Venus* communities with Spatangidae. These were subdivided into two series: Series A, found in finer deposits and characterized by *Chione* (*Venus*) *striatula* and *Echinocardium cordatum*; and Series B, found in coarse deposits and characterized by *Chione* (*Venus*) *fasciata* and *Spatangus purpureus*.

Of forty species listed in Series A, thirty are recorded from Great West Bay; whereas of eighteen in Series B, only two have been taken (*Nucula radiata* and *Chione fasciata*), each occurring at only one station. (*Glycimeris glycimeris* and *Laevicardium crassum*, both from Series B, have, however, been taken in dredgings about 3 miles south of Straight Point.)

In general, the 'SpVf' communities of Series B are poorly represented and very localized, while the 'EcVg' communities of Series A are characteristic of the area. Ford has divided the 'EcVg' communities into subcommunities, but this has not been attempted for this area.

A number of species which are scarce or localized at Plymouth but common in the Bay may be noted: *Spisula solida*, *Turritella communis*, *Lutraria lutraria*, *Tellina fabula*, *Pectinaria* spp. and *Cerianthus lloydi*. Differences in the fauna of the two areas may be due to the greater shelter, deposition of large quantities of mud, or to the presence of a different type of bottom in the Bay.

With regard to the last, it seems possible that certain members of the fauna may prefer the type of sand found in the Bay to that off Plymouth. In the Bay much of the sand is derived from erosion of Permo-triassic red sandstone, of desert origin, which produces sand grains which, although angular, are more or less isodiametric (see, for example, Wilson, 1948, pl. XVI, fig. 3). Off Plymouth, however, one may assume that the sand is mainly derived from the marine-eroded Palaeozoic rocks, and the grains can be seen to present a more irregular outline, rather like the 'gritty sand' described by Wilson (1948, pl. XVII, fig. 3). It is possible that the distribution of *Pectinaria* spp., for example, is controlled by its preference for the type of sand found in Great West Bay, since it constructs its tube of sand grains.

Of species present at Plymouth but absent from the Bay one may merely list species of the 'SpVf' association. Their absence is due to the lack of coarse deposits which are associated with a strong tidal scour.

Note on *Crepidula fornicata*

Although not taken in the bottom-sampler hauls, the spread of *Crepidula fornicata* (L.) to the area may be noted. Its occurrence in the Torquay-Paignton-Brixham area is mentioned by Cole (1950). In August 1948 a single specimen was found on a whelk shell taken south of Straight Point, and since then the species seems to have increased in numbers. Although the shores of Dawlish Warren and Exmouth have been frequently visited in the past few years, no shells of *Crepidula* were found until January 1950, when a number of empty whelk shells washed up on Dawlish Warren were found to have living *Crepidula* attached. Most were quite small, a centimetre or two in length, and several chains of three or four individuals were taken.

Summary

An account is given of the bottom-fauna of Great West Bay from samples taken in 1948 with a new sampler. Comparison is made with a similar survey made by Mr E. Ford with the Petersen grab in 1923.

The deposits contain a fair proportion of mud, and the 'EcVg' communities defined by Ford dominate the area. Within the Bay are found fairly dense beds of *Turritella communis*, *Lutraria* sp., *Callianassa subterranea* and *Spisula solida*.

No marked changes in the fauna seem to have occurred since the earlier survey. The fauna is briefly compared with that of the Plymouth area.

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Appendix

Table XI. Mr Ford's Stations (1923). S.S. *Salpa*

$\frac{1}{10}$ m.^{2} *Petersen grab.*

F 14	13. xi. 23	Hope Nose W½S, The Ness NW by W
15	,,	Hope Nose S, Babbacombe Pt. W by S
16	,,	Babbacombe Pt. S, Petit Tor NW
17	,,	Orestone S½W, Babbacombe Pt. W by S½S (Berry Head over Flat Rock)
18	,,	Babbacombe Pt. SW½S, The Ness N½E
19	,,	The Ness N, Hope Nose S by W
20	,,	The Ness NW, Orestone S by W
21	,,	Black Hd. SW, Babbacombe Pt. NW by W
22	,,	Flat Rock SW½W, Black Hd. NW¼W
23	14. xi. 23	Orestone NW by W½W, The Ness N by W¼W
31	15. xi. 23	Saltern Cove NW, Churstone Pt. SW by W½W
32	,,	Red Cliff Hotel NW by N, Roundham Hd. NW by W½W
33	,,	Orestone E by N, Torquay Pier N by W
34	,,	Thatcher Rock N, Orestone NE by N
35	,,	Berry Hd. S, Brixham Breakwater Light SW by W
36	,,	Brixham Breakwater Light WSW, Berry Hd. SE
37	,,	Brixham Breakwater Light SE by E, Old Battery SW
38	,,	Quarries WNW, Fishcombe Pt. S½E
39	16. xi. 23	Clerk Pt. W by N, Straight Pt. N by E
58	20. xi. 23	Berry Hd. N, 5 miles (log)
59	,,	Berry Hd. N, 10 miles (log)
60	,,	Start Pt. W by N¾N, Downend Beacon N by E¾E

N.B. Ford's positions are compass bearings, magnetic variation in 1923 being 15′ 05″ W.

TABLE XII. 1948 STATIONS. R.V. *SABELLA*

		$\frac{1}{10}$ m.² *Scoop-sampler*	
1	29. vii. 48	Exmouth Church	349°, 1·2′
2	,,	,,	349°, 1·7′
3	,,	,,	348°, 2·2′
4	,,	,,	349°, 2·7′
5	,,	,,	349°, 3·3′
6	,,	,,	349°, 3·8′
7	,,	,,	349°, 4·3′
8	,,	,,	349°, 4·8′
9	,,	,,	349°, 5·3′
10	,,	,,	349°, 5·8′
11	,,	,,	349°, 6·2′
12	30. vii. 48	Langstone Point	334°, 0·35′
13	,,	,,	334°, 0·75′
14	,,	,,	334°, 0·55′
15	,,	,,	022°, 0·55′
16	,,	,,	013°, 0·9′
17	,,	,,	017°, 1·15′
18	,,	Teignmouth Pier	229°, 1·7′
19	,,	,,	251°, 1·7′
20	,,	,,	324°, 0·6′
21	30. vii. 48	,,	004°, 1·9′
22	,,	Orestone	210°, 2·2′
23	,,	,,	222°, 3·5′
24	4. viii. 48	Berry Head	225°, 6·2′
25	,,	,,	254°, 5·7′
26	,,	,,	280°, 5·8′
27	,,	,,	297°, 6·4′
28	,,	,,	310°, 8·2′
29	,,	,,	319°, 9·4′
30	,,	Start Point	275°, 9·6′
31	,,	,,	282°, 6·3′
32	,,	,,	270°, 5·4′
33	,,	,,	240°, 5·6′
34	,,	,,	188°, 3·2′
35	,,	,,	181°, 3·3′
36	,,	,,	181°, 3·5′
37	,,	,,	182°, 3·7′
		Dredge hauls	
II	31. vii. 48	Hope Nose	177°, 1·6′
III	31. vii. 48	Teignmouth Pier	319°, 1·4′
XVI	3. viii. 48	Langstone Point	298°, 1·12′

N.B. The above are true bearings, and distances are in nautical miles.

BIONOMICS OF THE POOR-COD (*GADUS MINUTUS* L.) IN THE PLYMOUTH AREA

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(Plates I and II and Text-figs. 1–16)

CONTENTS

	PAGE
Methods of collection and treatment of material	186
Food of *Gadus minutus*	186
Age and growth determination in *Gadus minutus*	198
Age and rate of growth of *Gadus minutus*	219
The relation between the length and weight of *Gadus minutus* and its value as an index of the spawning season	228
Summary	235
References	236
Appendix: List of food organisms found in stomach contents of *Gadus minutus*	238

The Poor-Cod, *Gadus minutus* L., is a very common gadoid off Plymouth, 'probably the commonest gadoid in the trawling grounds' (Mar. Biol. Assoc., 1931). McIntosh & Masterman (1897) and Ehrenbaum (1901–10) have described its development, and Schmidt (1902–07) has given a very detailed description of its larvae and post-larvae. Barring these, and a few other scattered works on its systematics, no detailed study has been made so far on the general life-history of *G. minutus*. The scope of this work is limited to the food, age and rate of growth, the length-weight relation and the spawning period of the Plymouth poor-cod population. The great availability of this fish in the Plymouth area has made the problem of collection of material for this study quite easy.

I am greatly indebted to Mr F. S. Russell and Mr E. Ford for suggesting this problem to me and for giving me much help and criticism in my work. I am extremely grateful to Mr G. A. Steven for kindly going through the manuscript of this paper and for offering valuable criticisms and suggestions for its improvement. My thanks are especially due to Dr T. J. Hart who encouraged and helped me most generously throughout my work. I am grateful to Mr P. G. Corbin for lending me several post-larval specimens of *Gadus minutus* from his collections and to Mr G. M. Spooner for kindly identifying the amphipods[1] contained in the food of the fish. I am grateful to Dr M. V. Lebour and Dr D. P. Wilson for helping me in the identification of some of the crustaceans and polychaetes in the qualitative analysis of the food of the fish. To Mr F. G. C. Ryder my thanks are due for making the otolith measuring scale and the vertical projector. Finally my thanks are due to the

[1] See also p. 193 of this *Journal*.

entire technical staff of the laboratory and the crew of the laboratory vessels for their help in collecting the specimens.

The work described here was undertaken while I was holding the Madras Government Scholarship.

Methods of Collection and Treatment of Material

The whole material for this study has been collected from the Plymouth area outside the breakwater and around the Eddystone grounds by trawling from the Laboratory research vessels *Sabella* and *Sula*. The total number of fish thus collected and analysed is 5003 of all sizes ranging from 5 to 25 cm. Nearly all the specimens have been examined in the fresh state.

All specimens were measured to the nearest 5 mm., from the tip of the snout to the tip of the longest caudal ray (*total length*) and from the tip of the snout to the end of the caudal hypural (*standard length*).[1] It was apparent from the very beginning of the investigation that, because of the tearing and fraying of the caudal fin in trawled fish, all calculations had to be based on the standard length. All fish were weighed to the nearest gram in a Salter spring balance. The scales from the body of the fish which still retained them after trawling were removed by a scalpel and preserved in tissue-paper envelopes for later study. After measurements the specimens were dissected, the sexes were noted and the stomachs were then cut out and preserved in 5% sea-water formalin, sorted in 5 cm. body-length groups. A few random samples of specimens were boiled *in toto*. With other samples only the heads were boiled, for collecting the supra-occipital crest, which is the index that has been used for determination of age and rate of growth in this fish. During the early period of this study the specimens were collected by the ordinary otter trawl, and naturally a great amount of selective sampling by the gear has occurred. Towards the later period of the study Mr P. G. Corbin collected for me a fair number of O-group and I-group specimens of *G. minutus* by means of the otter trawl with attached sprat-net cod-end. The otoliths were collected by incising the skull dorsally behind the orbits and also by boiling the heads. All the otoliths were preserved in tissue-paper envelopes. A few specimens of the O-group from random samples were preserved in 5% sea-water formalin for later alizarine staining.

Food of *Gadus minutus*

The food has been analysed qualitatively and volumetrically. The stomachs of each 5 cm. length group of fish were kept separate as they were collected. Each stomach was subsequently dissected and the contents washed out into a Petri dish. The different organisms were sorted and their volumes measured. The volumes were determined by the displacement method in a measuring cylinder graduated to 0·1 c.c. The organisms were identified to species whenever possible. But the effect of digestion often rendered only the generic or family

[1] All the lengths of the fish given in this paper are *standard lengths*, unless otherwise stated.

characters recognizable. *G. minutus*, like several other gadoids, sometimes everts its stomach and disgorges its contents during the course of trawling. But this occurred only in 0·8 % of the stomachs analysed, and so could be assumed to have not interfered with the general conclusions. Another factor which also has to be taken into account in the analysis of the food organisms is the fortuitous snatching of other organisms while the fish are in the trawl. When the stomachs contained a few organisms which were quite fresh in appearance and showed no evidence of action of the digestive juices, their presence must be disregarded because of this habit, which is well known among many other fishes.

In the first few months of the study, the fish were grouped into 5 cm. groups for food analysis. It was soon found that there was virtually no apparent difference in the food ingested by the various adolescent year groups and so the work was done on two separate groups only; O-group and all the rest together.

In counting the food organisms several precautions had to be taken to avoid the numerical difficulties arising out of the pieces and fragments resulting from the different stages of digestion. The method suggested by Brown & Cheng (1946) was followed. For amphipods and polychaetes the heads were counted and only recognizable specimens of other organisms were counted, the residue being treated as '*Galathea* remains', '*Processa* remains, Fish remains', etc. Volumetric analysis helps to tide over this difficulty to a great extent.

Food of the I- to V-Year Groups

G. minutus of year-groups I to V is primarily a crustacean feeder, feeding on the bottom Crustacea. Day (1880–84) found that 'they live on small crustaceous animals...'. Thompson (1856) noticed chiefly Crustacea in their stomachs: 'In one was a full grown *Pagurus bernhardus* and fragments of marine plants also have occurred.' Fries *et al.* (1892) also make a more or less similar statement that 'it lives on small victims, consisting chiefly of crustaceans and mollusks'. In studying the food of the North Sea fishes, Franz (1910) found that the food of *Gadus minutus* consisted of fish (*Drepanopsetta*), crustaceans (*Pandalus* and *Eupagurus bernhardii*) and echinoderms.

In the analysis of the 3909 stomachs of Plymouth *Gadus minutus* (I to V year-groups) it was found that crustaceans form by far the greater part of the food consumed. Nine types of organisms form the principal food material of this fish in the Plymouth area. In the volumetric analysis (Tables I and II) these have been treated separately, and all the rest have been lumped together as 'others'. These nine principal organisms and their proportions of the total volume of food during the period under survey were as follows:

Processa canaliculata	21 %	*Porcellana* spp.	6 %
Fish	20 %	Crangonidae	6 %
Polychaeta	8 %	Amphipoda	3 %
Portunus spp.	8 %	Mysidacea and Euphausiacea	3 %
Galathea spp.	7 %		

Of the remaining 18% constituting the 'others', crustaceans formed 13%. Thus the total percentage of crustaceans consumed by the fish is 67 by volume.

When the number of fish that ingested particular organisms is considered, a different picture is obtained (Table III). *Processa canaliculata* occurs in more stomachs than any of the other food organisms, whose percentage frequency of occurrence is shown in the following list. Amphipods come second on the list, although as we have seen, they formed only a small percentage of the total volume of food. Conversely, Crangonidae and *Porcellana* spp., though forming a fair amount of the total volume of food, were found in a few fishes only. The reason is, of course, that whereas one *Porcellana* measured some 0·2 c.c., it requires 5–7 *Ampelisca spinipes* or 30–50 *Apherusa henneguyi* to make up the same volume.

29%	of the stomachs	contained	*Processa canaliculata*
23%	„	„	Amphipoda
16%	„	„	Fish
16%	„	„	*Galathea* spp.
14%	„	„	Polychaeta
10%	„	„	*Portunus* spp.
9%	„	„	*Porcellana* spp.
8%	„	„	Mysidacea and Euphausiacea
8%	„	„	Crangonidae

The average volume of food per stomach for the period of investigation was 0·5 c.c. The percentage of empty stomachs (without taking the number of everted stomachs into consideration) was 10·5. The average volume of food per stomach in the respective months during the period of study was as follows:

1948	c.c.	1949	c.c.
Apr.	0·57	Jan.	0·34
May	0·59	Feb.	0·43
June	0·54	Mar.	0·42
July	0·73	Apr.	0·69
Aug.	0·46	May	0·77
Sept.	0·49	June	0·59
Oct.	0·47		
Nov.	0·42		
Dec.	0·46		

Because the fish were collected at about the same time of the day throughout the investigation, it is probable that most of the food in their stomachs had undergone the same amount of digestion. The volume of food in the stomachs does not represent the volume consumed during feeding, because different food organisms will be digested at different rates. But on the general assumption that the food in most stomachs had reached the same state of digestion the results can roughly be treated as a fair guide to the feeding activity of the fish. On this basis three definite phases of feeding activity could be distinguished.

	1948									1949					
Food organisms	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
Fish	2·4	24·0	28·0	36·1	2·6	3·1	4·7	3·2	5·8	2·8	8·6	6·9	9·8	12·1	19·3
Amphipoda	2·0	2·6	3·2	2·0	1·7	1·4	0·7	1·7	1·5	0·6	0·5	1·0	1·4	1·4	1·7
Polychaeta	16·0	4·6	1·3	1·5	1·0	6·7	2·1	1·9	2·5	4·1	5·3	5·5	2·4	2·9	1·2
Schizopoda (*sens. lat.*)	2·4	3·0	2·8	1·0	1·0	1·0	1·0	1·0	1·0	1·0	0·5	0·4	0·8	1·4	2·2
Processa canaliculata	6·2	14·0	7·4	11·5	16·7	14·2	15·7	10·8	9·6	5·5	7·6	11·6	5·6	5·6	16·3
Crangonidae	8·1	2·2	2·0	3·0	2·9	2·1	1·1	4·5	5·6	3·3	1·8	0·7	1·0	2·6	1·1
Galathea spp.	2·4	3·6	4·0	4·3	3·8	2·2	3·1	1·3	3·5	1·9	3·2	3·8	14·2	4·6	4·8
Porcellana spp.	1·1	0·5	2·1	8·3	2·5	2·3	0·7	5·1	5·0	1·4	2·5	3·6	3·4	3·8	2·0
Portunus spp.	3·9	2·2	1·5	3·4	5·4	5·7	4·1	2·9	3·1	3·4	3·1	2·9	6·5	5·2	6·1
Others	12·0	2·0	1·6	1·6	8·4	9·9	13·9	9·9	8·2	9·7	9·4	5·5	24·2	36·9	4·6
Total volume	56·5	58·7	53·9	72·7	46·0	48·6	47·1	42·3	45·8	33·7	42·5	41·9	69·3	76·5	59·3
No. of stomachs examined	160	486	470	195	242	266	189	215	155	189	308	330	302	252	150
No. of empty stomachs	20	54	61	21	18	14	15	10	16	24	52	40	26	18	16

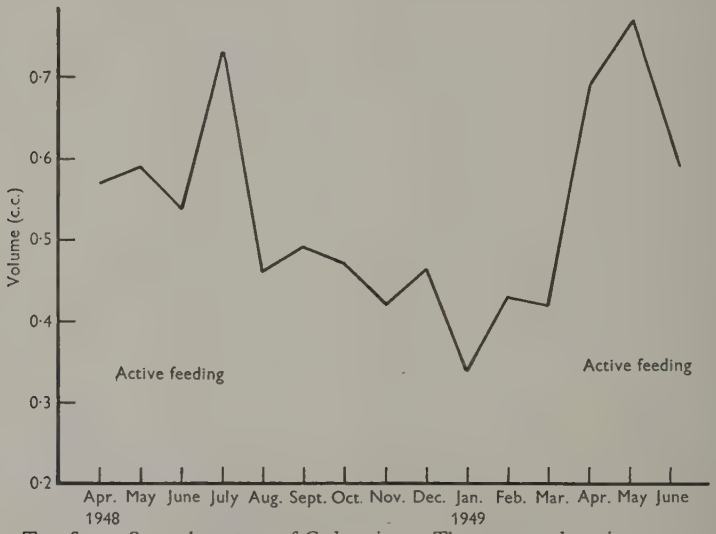
Table II. Percentage Composition of the Stomach Contents

	1948									1949					
Food organism	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
Fish	4·2	40·9	51·9	49·7	5·7	6·4	10·0	7·5	12·7	8·3	20·2	16·5	14·1	15·8	31·6
Amphipoda	3·5	4·4	5·9	2·8	3·7	2·9	1·5	4·0	3·2	1·8	1·2	2·4	2·0	1·8	2·9
Polychaeta	28·4	7·8	2·4	2·1	2·2	13·8	4·5	4·5	5·5	12·2	12·5	13·1	3·5	3·8	2·0
Schizopoda (*sens. lat.*)	4·2	5·1	5·2	1·4	2·2	2·1	2·1	2·4	2·2	2·9	1·2	1·0	1·2	1·8	4·1
Processa canaliculata	11·0	23·9	13·7	15·8	36·3	29·2	33·3	25·5	21·0	16·4	17·9	27·7	8·1	7·3	27·5
Crangonidae	14·2	3·7	3·7	4·2	6·3	4·3	2·3	10·6	12·2	9·9	4·2	1·7	1·4	3·4	1·9
Galathea	4·2	6·1	7·4	5·9	8·3	4·5	6·6	3·1	7·6	5·6	7·5	9·1	20·5	6·0	8·1
Porcellana	1·8	0·9	3·9	11·4	5·4	4·7	1·5	12·1	10·9	4·2	5·9	8·6	4·9	5·0	3·4
Portunus	7·1	3·6	2·8	4·7	11·7	11·7	8·7	6·9	6·8	10·2	7·3	6·9	9·4	6·8	10·3
Others	21·3	3·4	3·0	2·2	18·2	20·4	29·5	23·4	17·9	29·1	22·1	13·1	34·9	48·2	7·8

Table III. Percentage of Prevalence of the Food Organisms in the Stomachs Examined

	1948									1949					
Food organism	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
Fish	9·4	27·2	35·0	61·5	5·4	3·8	9·0	11·7	11·6	6·3	15·6	13·3	9·4	6·0	14·6
Amphipoda	9·4	39·5	36·6	27·7	20·7	15·0	8·5	23·3	9·0	9·5	5·8	10·9	8·7	16·3	27·0
Polychaeta	43·8	19·1	4·7	6·2	4·1	23·3	5·8	14·0	10·3	23·8	12·3	9·7	10·3	18·3	7·2
Schizopoda (*sens. lat.*)	12·5	30·3	11·1	8·7	9·1	6·0	4·2	9·3	5·2	4·2	5·2	3·6	1·7	1·2	9·3
Processa	28·1	34·6	43·8	24·6	48·8	45·1	26·5	34·9	22·6	20·6	11·7	19·4	13·2	20·6	38·5
Crangonidae	12·5	7·8	7·2	11·8	9·9	8·3	3·7	9·3	7·7	6·3	3·9	4·8	5·0	12·3	8·2
Galathea	9·4	16·7	12·1	13·8	14·5	15·8	12·2	14·0	13·5	7·9	7·1	31·5	33·7	24·2	10·7
Porcellana	3·1	2·9	2·3	7·7	4·1	6·0	4·2	16·3	12·3	7·9	11·0	18·2	16·2	14·7	5·6
Portunus	9·4	8·8	6·6	10·8	16·8	5·3	9·0	7·0	11·6	15·9	4·5	4·8	12·3	10·7	9·3

The average volume of food per stomach has been plotted against the respective months as a curve (Text-fig. 1). The spawning period of the fish is from February to May. Text-fig 1 makes clear that there was a period of very active feeding from April to July, synchronizing with the end of spawning and the period just after spawning when the fish was recovering from the strain. This was followed by a period, from August to December, when the average volume of food per stomach was more or less the same as the annual average volume per stomach. For practical purposes this period could be



Text-fig. 1. Stomach contents of *Gadus minutus*. The average volume in c.c. per stomach in successive months.

distinguished as 'the period of average feeding', and it coincided with the latter part of summer, autumn and early part of winter. This period was succeeded by a period of 'low feeding'. During the months just prior to spawning and during the earlier part of the spawning period, i.e. from the latter part of December to early part of March, the abdominal cavity of the fish is very much distended and filled by the gonads. At this time the fish shows a much reduced feeding activity. Just after spawning the fish feeds voraciously. Newly spawned and fully spent specimens with their stomachs gorged with food were common in the April and May samples. In May 1949 two specimens, measuring 19·5 and 20 cm., had ingested 6 and 5 c.c. of food material respectively. Both were emaciated and completely spent, and in each of them the supra-occipital stood out like a skin-covered crest on the top of the head. Such specimens were frequent in April and May.

This conclusion is substantiated further by the number of empty stomachs occurring in the various months. The percentage of empty stomachs that occurred in the respective months are given below:

1948	%	1949	%
Apr.	10·0	Jan.	12·7
May	11·1	Feb.	17·5
June	13·0	Mar.	12·1
July	10·5	Apr.	8·6
Aug.	7·5	May	7·1
Sept.	5·3	June	10·6
Oct.	7·5		
Nov.	5·0		
Dec.	10·0		

The percentage of fish with empty stomachs was greatest just prior to, and during, the spawning period. During the period of growth, i.e. from August to November, the percentage was small. Almost all the fish which had empty stomachs during the spawning months were fully mature specimens with ripe and enlarged gonads about to spawn.

The percentage of empty stomachs, if calculated for the three different periods of feeding activity, can be seen to average 10·1 % during the period of active feeding from April to July, 7·1 % during the period of 'average feeding' from August to December, and 14·1 % during the period of low feeding from January to March.

Considering the part that each of the principal food organisms plays in the food and feeding of the poor-cod, we find that *Processa canaliculata* is the commonest organism, forming a very large proportion of the food throughout the year. It is most predominant in the months following spawning, especially from August to November (Text-fig. 2A).

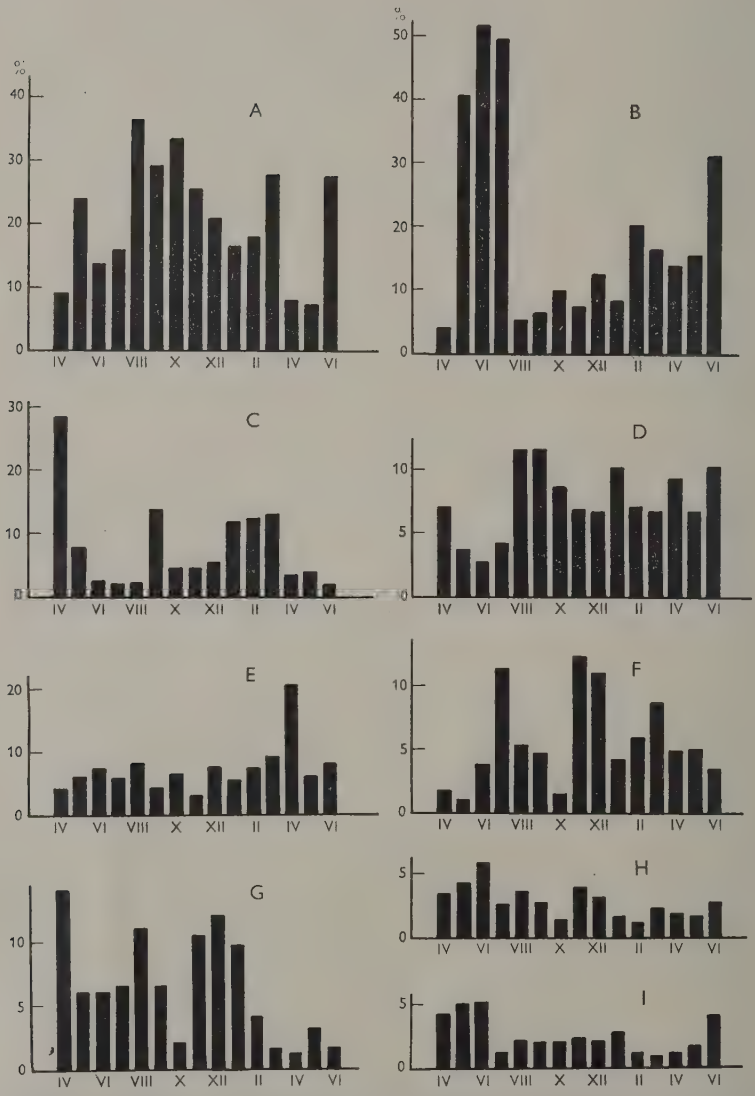
In August and September 1948 as many as 46 %, or nearly half the number of fish analysed, had ingested *Processa*. Only a few had this organism in their stomachs during the spawning period.

Fish. Fish forms an important portion of the diet of the poor-cod during May, June and July (Text-fig. 2B). Owing to advanced digestion it was not possible to identify the species of fish consumed in some stomachs. The otoliths were the best aid to identification. The fish found in the stomachs of the poor-cod were:

Crystallogobius nillsoni May, June, July 1948

Callionymus sp.
Trigla sp.
Ctenolabrus sp.
Gadus minutus? } February, March, April 1949

In July 1948 as many as 61 % of the stomachs analysed had fish in them. In June of the same year about 35 % had ingested fish.



Text-fig. 2. Histograms showing the relative percentage composition of the nine principal food organisms taken by *Gadus minutus* in the different months during 1948–49. For comparison all values are expressed as the percentage in volume of 100 c.c. of food material. A, *Processa canaliculata*; B, fish; C, Polychaeta; D, *Portunus* sp.; E, *Galathea* sp.; F, *Porcellana* sp.; G, Crangonidae; H, Amphipoda; I, mysids and euphausiids.

Polychaeta. Polychaetes have presented considerable difficulty in identification as they were in an advanced state of digestion in most of the stomachs. They were largely present in the food during the spawning months (Text-fig. 2C). *Amphitrite* sp. and *Goniada* sp. formed the commonest of the identifiable worms in the food. In September 1948 there was one stomach which contained a *Pallasia murata* with a portion of the worm in a part of the tube. In April 1948 nearly 40% of the stomachs examined had polychaetes in them.

Portunus sp. Portunidae were present in the food throughout, forming a fairly consistent proportion of it (Text-fig. 2D). In August and September 1948 they formed nearly 12% of the food in the stomachs analysed. The common species were *P. pusillus* and *P. depurator*. In August 1948 about 17% of the stomachs analysed had Portunidae.

Galathea sp. Galatheids form an important element of the crustacean part of the food, especially during the latter part of the spawning period, from March to May (Text-fig. 2E). Many of the spent fish in April 1949 had their stomachs distended and gorged with nothing but *Galathea*. *G. intermedia* was the commonest species, *G. dispersa* was also found fairly often, while *Munida bamffica* occurred twice. In March and April 1949 as many as 30% of the stomachs examined had *Galathea* in them.

Porcellana sp. *Porcellana* forms a small yet consistent part of the food, being most common in the months just prior to spawning (Text-fig. 2F). *P. longicornis* is the common species found in the stomachs of *Gadus minutus*, though occasionally *Porcellana platycheles* has been observed in fish of the younger year groups in April and May 1949. In November 1948 *Porcellana* was found in about 16% of the stomachs examined.

Crangonidae. Crangon vulgaris and *Philocheras bispinosus* were the two species usually found in the food. Crangonidae were especially common just before and after spawning (Text-fig. 2G). In April 1948 and May 1949 nearly 12% of the fish had ingested Crangonidae.

Amphipoda. Caprellidea (mainly *Phtisica marina*) were found in the stomachs more often in the months of April, May and June than in the other months, but Gammaridea formed a larger proportion of the amphipods consumed. The Gammaridea commonly found in the food were *Apherusa ovalipes*, *A. henneguyi*, *Ampelisca spinipes* and *A. diadema*. Mr G. M. Spooner informs me that *Phtisica marina* lives exclusively amongst hydroids and sponges and *Ampelisca* spp. are burrowers, usually lying buried under a surface layer of sand or gravel.

The occurrence of these amphipods in such large numbers in the stomachs of the poor-cod suggests a deliberate search on the part of the fish to ingest these forms and it further emphasizes the bottom-feeding nature of the fish.

Big specimens of *A. spinipes* measuring between 8 and 18 mm. in length were common in the stomachs in August and September 1948 and in March and April 1949. In August 1948 two specimens had in their stomachs

152 and 131 *Apherusa* spp. respectively. The proportion of amphipods in the total volume of food in the stomachs was comparatively small; yet a large number of fish had fed on them. In the latter part of the spawning season and in the months just following spawning the proportion of amphipods was larger than in other months (Text-fig. 2 H). Gammaridea were most common in July, August and September 1948. In May 1948 amphipods were found in about 40% of the stomachs examined.

Mysidacea and *Euphausiacea*. Schizopods form only a small proportion of the food of the fish, but were fairly consistent in their occurrence in the stomachs (Text-fig. 2 I). *Leptomysis gracilis* was the species most commonly ingested, and a few *Anchialina* were occasionally observed. In April and May 1948 a fairly large number of stomachs contained mysids and euphausiids (13% in April and 30% in May).

Others. Of the other organisms special mention should be made of *Upogebia* sp. and small Paguridae (mainly *Eupagurus bernhardus*). In May 1949 *Upogebia* formed as much as 36% of the total volume of food, and about 10% of the fish had them in their stomachs. Paguridae also formed a large proportion in the food (26% of the total volume) in April 1949 and as many as 15% of the fish had ingested them.

Isopoda, Mollusca and Echinodermata formed only a negligible proportion of the food throughout the year. Occasionally they formed a large proportion in the food of a few individual stomachs. But such instances were very rare.

The various organisms that were found in the analysis of the food of the poor-cod of the adolescent years are given in the Appendix (p. 238).

Thus *Gadus minutus* in its adolescent and adult stages is primarily a crustacean feeder, feeding on the bottom-living forms and showing differential feeding activity depending on spawning and growth.

Food of the O-Group of Gadus minutus

Comparatively few specimens of the O-group were available for study of the food and they have been obtained during seven months only, viz.:

	Specimens		Specimens
Oct. 1948	5	March 1949	22
Nov. 1948	159	Apr. 1949	3
Jan. 1949	21	May 1949	55
Feb. 1949	364		

All these specimens were between 7 and 9 cm. long (standard length). The numbers for October 1948 and April 1949 are negligible. The February 1949 and November 1948 collections alone are of any comparative value. The analyses of the food of O-group in the different months are not therefore strictly comparable. This food analysis is therefore restricted to an enumeration of the food organisms and a comparison with the food of the older age groups.

The poor-cod of the O-group also is primarily a crustacean feeder. Copepods, small *Galathea intermedia*, small *Porcellana longicornis*, and amphipods formed a large proportion of the food in all the seven months. Lebour (1919) also noted that the food of the poor-cod of a length from 40 to 160 mm. 'is chiefly crustacea—copepods, especially *Calanus* and *Temora*, *Podon*, decapods and their larvae....' But the earlier post-larval stages are evidently still plankton feeders.

The average volume of food per stomach was 0·12 c.c., compared with 0·5 c.c. in the older fish. Empty stomachs were found only in November 1948 and February 1949, and their percentages were only 3% in November and 5% in February.

The majority of the stomachs contained fine sandy gravel mixed with empty shells of very small *Natica* sp. and *Nucula* sp.

The volumetric analysis of the food and the percentage composition of the stomachs containing the respective food organisms have been tabulated in Tables IV and V.

The various organisms that were found in the food of the O-group are given in the Appendix (p. 239).

Copepods were taken in all the 7 months. About 90% of the stomachs examined had copepods in them. *Calanus finmarchicus* and *Acartia clausi* were the commonest. The others were *Temora* sp., *Pseudocalanus elongatus*, and *Centropages typicus*. When the stomachs had a large copepod content they usually presented a reddish colour. Copepods were especially noticeable in November 1948, February, March and May 1949.

Amphipods formed a great proportion of the food in November 1948, February and May 1949. Caprellidea were very rare. They were found only in 1·9% of the stomachs examined in the 7 months. Gammaridea formed almost the whole of the amphipodan element in the food. The species found were *Apherusa* sp. and juvenile forms of *Ampelisca diadema* and *A. spinipes*.

Galathea intermedia formed the greatest proportion of the food in January, February and March 1949. In January and March 1949 as many as 60% of the stomachs examined had *G. intermedia* in them. All the *G. intermedia* were small and juvenile forms. The other decapod crustacea found in the food were *Pandalina brevirostris*, *Philocheras bispinosus*, *Crangon vulgaris*, small *Porcellana longicornis*, small *Portunus* spp., *Eupagurus bernhardus* and small *Processa canaliculata*.

Mysids and euphausiids were found mainly in January 1949, when as many as 55% of the stomachs contained them. *Leptomysis gracilis* and *Nyctiphanes couchi* were the species taken.

In January 1949 many stomachs contained polychaetes mostly unrecognizable. The only identified species was *Goniada* sp.

Among Isopoda, *Conilera cylindracea* was taken from a few stomachs in November 1948 and February, March and May 1949.

TABLE IV. VOLUMETRIC ANALYSIS OF THE STOMACH CONTENTS PER 100 STOMACHS (VOLUME IN C.C.)

	O-group						
Food organism	Oct.	Nov.	Jan.	Feb.	Mar.	Apr.	May
Polychaeta	..	0·2	1·5	2·4	0·5	3·3	0·6
Mollusca	..	0·1	0·1	0·1	0·1	..	0·2
Isopoda	..	0·4	..	0·2	0·4	..	0·4
Amphipoda	2·0	2·4	0·8	1·4	0·8	..	1·8
Processa	4·0	0·4	0·8	0·4	1·0	..	0·4
Crangonidae	3·0	0·6	1·0	0·1	..	..	0·2
Galathea	6·0	2·8	5·0	4·1	3·0	6·6	1·0
Portunus	..	..	0·4	0·6	..	..	0·6
Porcellana	..	0·2	2·1	1·9	0·7	..	0·8
Baguridae	..	..	..	0·2	..	..	..
Copepoda	0·2	0·2	0·1	0·4	0·2	0·1	0·2
Schizopoda (*sens. lat.*)	..	0·4	0·4	0·3	0·2	..	0·2
Sandy gravel and stone	0·8	0·2	0·5	0·1	0·4	0·6	0·2
Others	0·4	0·8	0·9	1·0	1·7	..	0·7
Total volume in c.c.	16·4	8·7	13·6	13·2	9·0	10·6	7·3
No. of stomachs examined	5	150	21	350	22	3	55

TABLE V. PERCENTAGE OF PREVALENCE OF THE FOOD ORGANISMS IN THE STOMACHS EXAMINED

	O-group						
Food organism	Oct.	Nov.	Jan.	Feb.	Mar.	Apr.	May
Polychaeta	..	2	55	12	23	66	9
Mollusca	..	10	20	3	23	..	46
Isopoda	..	3	..	1	20	..	8
Amphipoda	100	16	75	18	70	..	32
Processa	20	3	10	1	15	..	4
Crangonidae	20	3	10	2	..	..	4
Galathea	60	28	60	40	65	100	10
Portunus	..	..	5	4	..	..	4
Porcellana	..	2	20	10	25	..	6
Paguridae	..	..	..	1	..	..	..
Copepoda	100	72	100	92	95	100	76
Schizopoda (*sens. lat.*)	..	12	55	6	20	..	8
Sandy gravel and stone	100	66	80	29	85	66	62

Lebour (1917, 1919) examined the food of 144 post-larvae measuring 6–14 mm., and fifty-three specimens of the O-group of *Gadus minutus* in 1917 and 1919. The records of her analysis of the food of these fish were as follows:

140 specimens of *G. minutus* post-larvae measuring 6–14 mm., from the Young Fish Trawl of 1914, were examined (Lebour, 1917, p. 455). Of these 4 stomachs were empty, 1 contained ova, 1 contained *Dinophysis*, 134 contained *Pseudocalanus elongatus*, with *Acartia*, *Euterpina*, *Metrida* and *Podon* each occurring once.

In 1919, 4 specimens of 6–13 mm. long post-larvae and 53 specimens of the O- and I-groups of *Gadus minutus* were examined (Lebour, 1919, pp. 283–5).

Analysis of the post-larvae: one empty, two contained copepod remains, one contained 1 *Pseudocalanus* and one young *Temora*.

Analysis of the O-group and I-group:

No. of specimens	Length in mm.	Food
1	40	*Crystallogobius*, many *Podon*, *Calanus*, *Temora*, remains of decapod larvae
3	60–70	Crustacean remains, many *Acartia*, *Candacia*, *Temora*, decapod larvae, young amphipods and isopods
5	70–80	*Temora*, *Candacia*, decapod larvae remains, *Calanus* and one empty
5	80–90	Copepod remains, *Calanus*, *Pseudocalanus*, decapod larvae, *Candacia* and *Eupagurus* larvae.
8	90–105	Copepod remains, annelid remains, *Pandalus montagui* and decapod remains
19	73–105	Indistinguishable
5	69–110	*Crangon* remains
1	135	*Labidocera wollastoni*, many *Calanus*
1	143	4 *Crystallogobius*, mysid, and many *Calanus*
5	83–160	Decapod remains (*Leander*?)

Only three post-larvae of *Gadus minutus* occurred in the present material and all of them contained *Pseudocalanus* in their stomachs. Lebour's analysis of the food of 144 post-larvae quoted above showed that the great majority contained copepods, amongst which *Pseudocalamus elongatus* was always present. Other species each occurred once only. It is quite evident, as Lebour emphasizes, that *Pseudocalanus* is the favourite food of *Gadus minutus* in its post-larval stages.

Lebour's analysis revealed that the food of *G. minutus* contained fish and crustacea at the respective stages as follows:

6–14 mm. (total length)	40–105 mm. (total length)	105–160 mm. (total length)
Copepods, ova, *Dinophysis*	Copepods, amphipods, isopods decapod larvae, *Pandalus montagui*, *Podon*, *Crystallogobius*, *Crangon*	*Crystallogobius*, *Leander*?, *Crangon*, mysids

Lebour further stated that *Gadus minutus* 'in their young stages eat *Pseudocalanus* more than anything else, *Acartia* and other small copepods also being taken, probably when *Pseudocalanus* is not so abundant. *Calanus* is taken by the larger but rarely by the smaller fish.'

The present analysis also reveals this fact well. The O-group (7–9 cm. standard length) contained copepods, amphipods and small decapods like *Galathea intermedia*, *Porcellana longicornis* and small *Portunus* spp. besides occasional inclusions of polychaetes, mysids, and isopods. There was a complete absence of fish in the food analysed. Even Lebour found fish in only two specimens of the sample, one of which was 14·3 cm. in total length and therefore belonged to the I-group. Thus copepods, amphipods and *Galathea* formed the bulk of the food of the poor-cod of the O-group.

In the food of the I–V groups the bigger decapods like *Processa canaliculata*, *Portunus* sp. and *Galathea* spp., and fish like *Callionymus* sp., *Trigla* sp. and *Crystallogobius* sp., and polychaetes formed the major portion throughout the year. Copepods were observed only in four stomachs in the food analysis of

these age groups. It is quite evident that copepods do not play any important part in the food and feeding of the fish at this adolescent and adult period of its life.

The food of *G. minutus* can thus be divided into three categories depending on the three phases of its life cycle, as follows:

Stage	Length in mm. (Standard length)	Food
Post-larval	6–14	Copepods, mostly *Pseudocalanus elongatus*
O-group	40–80	Copepods, mostly *Calanus finmarchicus*, *Acartia* and *Temora*; small decapods like *Galathea intermedia*, *Porcellana longicornis*, etc.; amphipods, mostly Gammaridea; isopods and polychaetes
Adolescent and adult stages	80–230	Decapods, mostly the larger like *Processa canaliculata*, *Galathea* sp., *Portunus* sp., *Porcellana* sp., *Upogebia*; fish like *Crystallogobius* and *Callionymus* sp.; polychaetes, mostly *Amphitrite* and *Goniada*, amphipods like large *Ampelisca* spp., *Apherusa* spp. and *Phtisica marina*

Age and Growth Determination in *Gadus minutus*

In his studies of the rate of growth of Plymouth fishes Cunningham (1891) made some observations on the growth rate of *Gadus minutus* from length measurements. He examined 246 specimens collected between 1889 and 1891. After that J. S. Thomson (1904) used the scales of *G. minutus* in his investigation on the validity of scales as an index of age in Gadidae. Apart from these two early investigations there is no other reported work on the age determination and growth rate of this species.

The scales of *G. minutus* are very deciduous and get scraped off from the body of the fish very easily during trawling. Even with specimens which retain a few scales, it is quite impossible to collect them from the same region of the body in all of them. Again, very often the retained scales turned out to be the minute scales which Stuart Thomson (1904) has described in his paper. Harold Thompson (1922) has shown in his treatise on haddock scales how essential it is to collect the largest scales, and that too from one and the same region in all the specimens, if any assessment of age and if any valid and reasonable comparison between the several specimens can be made. In the present work the scales were used for deciphering the age only in the relatively few specimens where this was possible. They could not be used for any assessment of back-calculation and growth rate. For age determination in *G. minutus*, the otoliths at first were used. The otoliths are very massive and thick structures, and to reveal the 'year rings' they had to be broken transversely and sometimes even sectioned before the rings could be distinguished. Though the zones were quite clear in most of them there was no uniformity in the width of the zones, and it was not practically possible to make sections at the same sagittal plane in all the otoliths. For these reasons it was impossible to utilize the otolith for critical comparisons and for purposes of back-calculation. Therefore some other structure had to be selected for a satisfactory

estimation of the age and growth rate, possessing all these necessary traits of an 'age index'. The supra-occipital crest was selected with this in view.

Bones have rarely been used for age determination of marine fishes and even when they have, there have been differences of opinion on the validity of the zones, as is clear from a survey of the literature (Menon, 1950). The main objection against utilizing bones for age assessment has been that the zones are ill-defined. This difficulty can usually be overcome by finding out the optimum temperature for cooking the specimens when collecting the bones. Overcooking always blurs the zones. When the bones are prepared without overcooking it is found that age assessments can be based on them with at least as much confidence as on scales or otoliths.

Growth rate from scales

Scales were collected from all specimens in which they were available. Only those scales which were firmly lodged in the scale pockets were collected as, being extremely deciduous, there was a possibility of scales from different specimens getting intermingled on the fishes when they came up in the trawl. These scales were removed with a scalpel and stored in labelled envelopes. Altogether scales were collected from 294 specimens, from whichever region of the fish they were remaining in their pockets. The scale of *G. minutus* has a thin shining dermal tissue covering it, often with big stellate chromatophores. These obscure the sclerites and it is necessary to clean the scale before it can be read under the microscope clearly. The best method of cleaning the scale is to put it in a solution of 10% caustic potash for 5 min. and then to scrape it in water in a watch-glass with a forceps and a needle. All the dermal tissues and chromatophores can easily be removed by this method. The scale is then mounted on a slide. The treatment with caustic potash imparts a deep black tinge to the sclerites, which thus become clearly defined and visible in the general field of the scale. Alizarine stain also enhanced the clarity of the sclerites and 'rings'. After removal of its chromatophores and dermal tissues the scale is placed in alizarine staining solution for 5 min.[1] The excess stain is washed off by leaching the scale in 2% caustic potash solution, and then the scale is mounted in glycerine. The 'annual rings' become very clearly defined. This method was better, easier and quicker than that suggested by Graham (1929*a*).

The scale of *G. minutus*, like the scales of most Gadidae, is oval in shape, with several sclerites arranged around a central nucleus (Pl. II, fig. 1). The sclerites are arranged in alternating bands of widely separated ones, which constitute the so-called 'summer zone' and of closely approximated ones, which constitute the 'winter zone or ring'.

[1] Alizarine staining solution: 5% caustic potash, 1000 c.c.; alizarine dye solution, 1 c.c. Alizarine dye solution: glacial acetic acid, 0·5 c.c.; glycerine, 3 c.c.; chloral hydrate 10 c.c. and alizarine sulphonate 0·1 g.

The difficulty of getting scales from the same region of the fish in all specimens has been explained in the preceding paragraphs. They are therefore not comparable in size. The measurements of these scales made with a micrometer scale verified that there is no regularity in the measurements of scales from the different specimens. The zones are very clearly defined in stained scales and fairly distinguishable in unstained ones. Unfortunately, no data of blank scales were kept and so a probable or approximate percentage of them

TABLE VI. ANALYSIS OF THE SCALES OF *GADUS MINUTUS* ACCORDING TO THE LENGTH- AND AGE-GROUPS

Length in cm.	Year groups: Male 1−	1+	2+	3+	4+	Female 1−	1+	2+	3+	4+	5+	Total
7·5	3	..	..	..	..	3	..	..	..	..	..	6
8·0	3	..	..	..	..	4	..	..	..	..	..	7
8·5	5	2	..	..	..	4	3	..	..	..	..	14
9·0	1	5	..	..	..	1	4	..	..	..	..	11
9·5	..	4	..	..	..	..	5	..	..	..	..	9
10·0	..	5	..	..	..	1	2	..	..	..	..	8
10·5	..	3	..	..	..	..	2	..	..	..	..	5
11·0	..	1	..	..	..	..	3	..	..	..	..	4
11·5	..	..	..	..	..	..	..	..	..	..	..	0
12·0	..	1	..	..	..	..	1	..	..	..	..	2
12·5	..	5	3	..	..	..	..	..	..	..	..	8
13·0	..	2	4	..	..	..	2	..	..	..	..	8
13·5	..	3	8	..	..	..	4	4	..	..	..	19
14·0	..	3	15	1	..	..	3	2	..	..	..	24
14·5	..	1	9	1	..	..	4	8	1	..	..	24
15·0	..	..	3	3	1	..	4	18	5	..	..	34
15·5	..	..	..	3	..	..	2	9	1	..	..	15
16·0	..	..	..	1	1	..	..	17	4	..	..	23
16·5	..	..	..	2	1	..	..	14	3	..	..	20
17·0	..	..	..	..	1	..	..	5	4	..	..	10
17·5	..	..	..	..	..	..	..	2	7	1	..	10
18·0	..	..	..	..	..	..	..	2	6	..	..	8
18·5	..	..	..	..	..	..	..	..	5	..	..	5
19·0	..	..	..	..	..	..	..	..	7	2	..	9
19·5	..	..	..	..	..	..	..	..	4	3	..	7
20·0	..	..	..	..	..	..	..	..	1	2	1	4
Totals	12	35	42	11	4	13	39	81	48	8	1	294
	104					190						

in the specimens examined cannot be given, but their proportion was high. There were several instances of false rings in the scales and with all these the age had to be checked by reference to the otoliths and supraoccipital.

The data of measurements of the scales are not given since they are not comparable. In Table VI are shown the various 5 mm. groups, the two sexes separately, divided up according to the number of 'closely arranged sclerite zones' or 'annual rings' in the scales that have been examined.

From Table VI it is quite evident that there is a different rate of growth in the two sexes. The majority of male *G. minutus* are more than 1 year old

when they reach a length of 9 cm., past 2 years at a length of 13 cm., past 3 years when they reach a length of 15·5 cm. and past 4 years at a length of 16·5 cm. In the same way the majority of females are past 1 year at 9 cm., past 2 years at 14·5 cm., past 3 years at 17·5 cm., and past 4 years at 20 cm. Thus at the end of the 1st, 2nd, 3rd and 4th years the fish reaches approximate lengths of 8·5–9, 12·5–13, 15–15·5, and 16·5–17 cm. in the male and 8·5–9, 14–14·5, 17–17·5 and 19·5–20 cm. in the female respectively. If we take the mean of each year's length range as the nearest approximation to the actual length, the average fish reaches the lengths shown in Table VII at the end of each year in the male and female respectively.

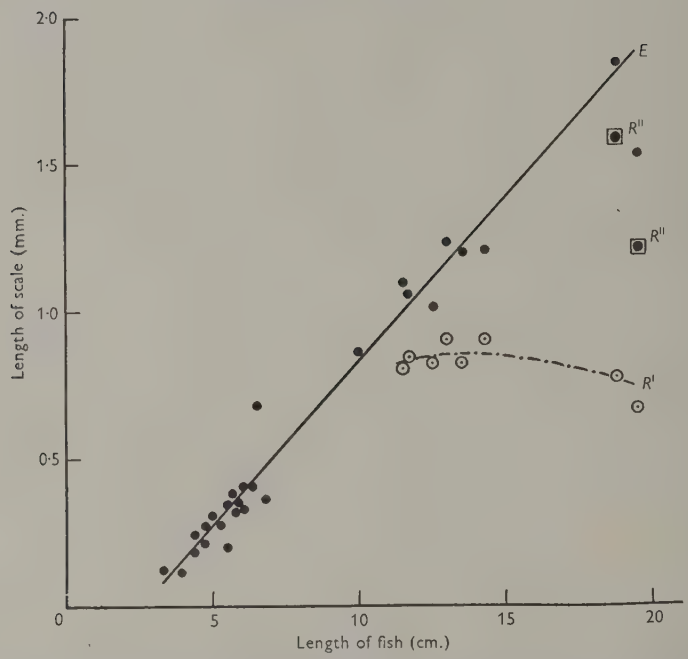
These average or 'mean' lengths are equivalent to the 'calculated lengths' given on p. 219.

Stuart Thomson examined the scales of fifty-six specimens ranging from 3·3 to 19·5 cm. (total length). He counted the number of sclerites in each zone and found the width of each annual zone by measuring along the long axis the distance from the centre of the scale of 'the nucleus' to the outer edge of

TABLE VII. AVERAGE LENGTHS (CM.) AT DIFFERENT AGES

At the end of	Male	Female
1st year	8·75	8·75
2nd year	12·75	14·25
3rd year	15·25	17·25
4th year	16·75	19·75

each 'ring'. The results have been given as a correlation curve in Text-fig. 3. In the graph the distance from the centre of the scale to its outer edge is plotted as curve *E*. The line R^{I} and the points R^{II} are the distances from the centre of the scale to the first and second rings, i.e. the annual growth of the scale in the 1st and 2nd years. Thomson did not separate the sexes, and his data cannot be analysed from that aspect. Also he measured no scales of fish between lengths of 6·8 and 10, 14·3 and 18·8 and above 19·5 cm. Yet his data reveal certain interesting details. It can be seen from the graph that *G. minutus* is past 1 year when it reaches a length of 10 cm. (total length) and just past 2 years when it is 15·87 cm. (total length). Thomson noted that a fish of 19·36 cm. (total length) is just past 3 years. Converting these lengths into standard lengths for comparing them with the writer's observations, they become 9, 14 and 17·2 cm. approximately. Thomson examined scales from the median region of the flanks slightly posterior to the pectoral fin and either slightly above or below the lateral line. His data for the fish above 19·36 cm. (total length) give very conflicting results, as all these fish are said to be above 2 and below 3 years. That fish of 23·5 and of 19·36 cm. (total length) are not of the same year class is clear—because, while the growth in the 1st, 2nd and 3rd year is 10, 5·87 and 3·49 cm. (total lengths) respectively, decreasing systematically every year, if the group 19·36–23·5 cm. belongs to the same year group, viz. the 4th year group, it means that the growth in the 4th year is greater



Text-fig. 3. The length in mm. of the scale from its 'centre' to its 'edge' at the different lengths of fish (data from J. S. Thomson, 1904). ●, measurements of the scale from the centre to the edge (E); ⊙ measurements of the scale from the centre to the first ring (R^{I}); ◙, measurements of the scale from the centre to the second ring (R^{II}).

Table VIII. Thomson's Measurements of *Gadus minutus* Scales

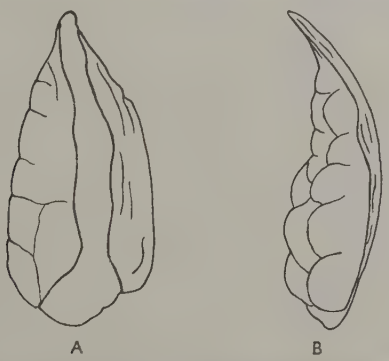
Total length in cm.	Average length of scale in mm. from centre to growing edge	Average no. of sclerites			Approximate age
		1	2	3	
3·3	0·12	0	..	..	3 months
3·9	0·21	4	..	..	3 months
5·0–5·9	0·34	7	..	..	3 months
6·0–6·8	0·47	8	..	..	3 months
10·0	0·86	23	..	..	1 yr. 1 month
11·5–11·7	1·07	30	9	..	1 yr. 3–4 months
12·5–14·3	1·18	29	11	..	1 yr. 3–4 months
15·87	Not taken	..	..	..	2 yrs. 1 month
17·14–18·09	Not taken	..	..	..	2 yr. 7 months approx.
18·80	1·84	26	25	11	2 yr. 3–4 months
19·36	Not taken	..	..	..	3 yr. 1 month
19·50	1·53	19	21	16	About 3 yr.
19·68	Not taken	..	..	..	Under 3 yr.
20·32	Not taken	..	..	..	2 yr. 1 month
22·22	Not taken	..	..	..	1 yr. 11 months
23·75	Not taken	..	..	..	2 yr. 11 months

than the 3rd year. This evidently suggests that the 19·36–23·5 cm. length group must have really consisted of more than one year group. This conflicting result in the data of Thomson must have arisen from the difficulty of reading the scales of older age groups. Thomson's data are summarized in Table VIII.

Thus from Thomson's data one finds that the length-groups 3·3–10 and 10–15·87 cm. belong to O- and I-groups respectively. Above 15·87 cm. the results are not very definite. As far as the O- and I-groups are concerned, Thomson's values agree quite well with the present results. In the writer's experience, above the I-group the sclerites become very close and crowded, and in the few scales that were examined there was great difficulty in identifying the rings. In most of them the rings could not be satisfactorily discerned without the previous knowledge of the probable age of the fish from the supra-occipital or the otolith. It must have been this evident overcrowding and narrowing of the sclerites that forced Thomson to overlook the rings after the first 2 years.

Growth rate from the otolith

The otoliths were collected by making a vertical cut in the skull behind the orbit and bending the front portion of the skull as suggested by Hickling (1933). When the heads alone were boiled they were collected after boiling and removing the supra-occipital. No change, or difficulty in reading the otoliths,



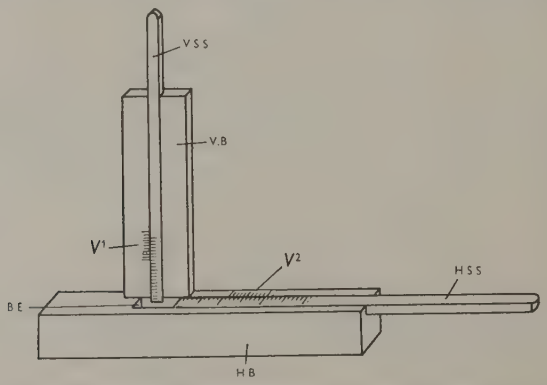
Text-fig. 4. Diagram of the otolith of *Gadus minutus* showing (A) its dorsal aspect and (B) its sagittal aspect.

of boiled specimens was found. The otolith of *G. minutus* is roughly drop-shaped with a slight concavity on its ventral side (Text-fig. 4). The posterior end of the otolith is bulbous and the anterior end tapers to a blunt point which bends downwards in the natural position.

On the dorsal surface there is a fairly broad but shallow acoustic canal. The ventral surface is rugose and has several thick and massive bulbous excrescences. These bulbous swellings are especially massive towards the middle and

posterior end of the otolith. They contribute to the thickness and mass of otolith, and make it impossible to read the otolith without cutting it. For age determination the otolith is cut transversely at about its widest and thickest region. The cut surfaces are then moistened with water, or glycerine, or even better with saliva, when they show the opaque and translucent bands clearly. With several it was found necessary to make ground sections, as in rock-sectioning, to read the zones clearly and satisfactorily (Plate II, figs. 2, 3). The method of grinding employed was much as suggested by Johnston (1938), with the only difference that the grinding was performed by hand with the aid of carborundum and a ground-glass plate.

The length and greatest thickness of the otolith were measured with a scale made for the purpose (Text-fig. 5). This consists of two small rectangular blocks of wood attached at right angles to one another. Each block has



Text-fig. 5. The otolith measuring scale (not drawn to scale). H.B. and V.B., the horizontal and vertical blocks; H.S.S. and V.S.S., the horizontal and vertical sliding scales; V^1 and V^2, the verniers; B.E., the blind end of the groove.

a groove, 7 mm. wide, running along its length up to the junction between the two blocks. The groove is shallow and wide enough to receive the widest and thickest otolith of *G. minutus*. Sliding wooden scales as wide and high as the grooves work in each. These scales may be called the 'vertical' and 'horizontal' scales. The blocks are so fixed to each other that the end of the vertical scale dips and fits into the horizontal groove at its blind end. The zero end of each scale is towards its outer end. Towards the zero end of each scale there is a vernier scale on the border of the groove. The otolith, when being measured, is placed at the blind end of the horizontal groove with its rugose side upwards. The horizontal scale is then moved towards the blind end until it holds the otolith firmly and straight. The length of the otolith can then be read on the horizontal scale and its vernier. To measure the thickness of the otolith, the

horizontal scale is released and the otolith is so adjusted, lying in the same position, as to place its thickest portion just beneath the 'dipping end' of the vertical scale. The vertical scale is then moved down to hold the otolith rigidly and the thickness is read on the vertical scale and its vernier.

The whole procedure is easy and rapid. It avoids the difficulties one encounters with an ordinary metal screw-guage or vernier, where there is the possibility of the blunt end of the otolith breaking and of not taking the measurements at the longest axis. The readings with the scale just described are as accurate as those with a screw-guage or vernier since it is possible to measure in mm. up to two decimal places.

As many as 600 otoliths were measured with this scale and the data revealed certain interesting points.

There is virtually no correlation (i) between the length of the fish and the length of the otolith, or (ii) between the length of the fish and the thickness of the otolith. There is no correlation (iii) between the length and thickness of the otolith, or (iv) between the otolith measurements and the sex or age of the fish.

There is no particular rule for the calcium accumulations of the otolith. An otolith of a 2-year-old fish may be as long and thick as that of a 3- or even 4-year-old one. Again, the otoliths of fish of the same age may show very different dimensions, the range of variation being quite big. This makes it difficult to compare the otoliths of fish of the same age or the same length or the same sex.

This fact was again revealed by the few measurements made of the width of the zones of the otolith. These are not published, because several sources of error seemed unavoidable. For example, it is not possible to cut the sections in precisely the same sagittal plane in all the otoliths, so that the measurements are not strictly comparable with one another. Instead the fish have been tabulated in 5 mm. length groups, against their age as assessed by the number of annual zones in the otoliths only, and treated in the same way as with the data relating to the scale readings (Table IX). From this it appears that the majority of male fish are past their first year when they reach a length of 10 cm., past 2 years at 13·5 cm., past 3 years at 16 cm., and past 4 years at 17·5 cm. The corresponding lengths for females were 10, 15, 18 and 19·5 cm. If the means are then calculated as with the data for scale readings, we get the 'calculated lengths' of the fish shown in Table X.

The zones in the otolith become very crowded at the periphery of the sections in the older age groups and it becomes a difficult problem to differentiate the various zones. False zones and 'doubled zones' are very prevalent. The massive nature of the otoliths and the lack of correlation in their measurements leave them useful only for direct age reading (even this is trustworthy only for the first two year-groups). Their zonations cannot be used for back-calculation.

TABLE IX. ANALYSIS OF THE OTOLITHS OF *GADUS MINUTUS* ACCORDING TO THE LENGTH AND AGE OF THE FISH

Length of fish in cm.	Age in years: Male 1−	1+	2+	3+	4+	5+	Female 1−	1+	2+	3+	4+	5+	Total
7·0	11	..	..	..	..	..	13	..	..	..	..	..	24
7·5	15	..	..	..	..	..	10	..	..	..	..	..	25
8·0	12	2	..	..	..	..	9	1	..	..	..	..	24
8·5	19	5	..	..	..	..	23	4	..	..	..	..	51
9·0	13	9	..	..	..	..	14	8	..	..	..	..	44
9·5	11	9	..	..	..	..	12	10	..	..	..	..	42
10·0	7	18	..	..	..	..	11	14	..	..	..	..	50
10·5	6	13	..	..	..	..	5	18	..	..	..	..	42
11·0	2	14	..	..	..	..	1	11	..	..	..	..	28
11·5	..	9	..	..	..	..	1	15	..	..	..	..	25
12·0	1	4	1	..	..	..	..	5	..	..	..	..	11
12·5	..	4	1	..	..	..	..	9	..	..	..	..	14
13·0	..	3	1	..	..	..	..	9	..	..	..	..	13
13·5	..	6	18	..	..	..	..	9	..	..	..	..	33
14·0	..	2	15	..	..	..	..	21	11	..	..	..	49
14·5	..	8	29	..	..	..	..	30	37	..	..	..	104
15·0	..	1	22	5	..	..	1	11	25	..	..	..	65
15·5	..	1	49	23	..	..	..	10	23	..	..	..	106
16·0	..	2	7	19	1	..	..	5	38	1	..	..	73
16·5	..	1	1	10	..	..	..	6	41	5	..	..	64
17·0	..	..	2	9	4	..	..	4	23	7	1	..	50
17·5	..	..	1	4	11	..	..	..	11	6	..	..	33
18·0	..	..	..	..	1	1	..	..	1	7	1	..	11
18·5	..	..	..	..	..	1	..	..	2	15	2	..	20
19·0	..	..	..	..	..	..	..	..	1	11	9	1	22
19·5	..	..	..	..	..	..	..	..	..	7	23	15	45
20·0	..	..	..	..	..	..	..	..	..	1	2	2	5
20·5	..	..	..	..	..	..	..	..	..	..	10	..	10
21·0	..	..	..	..	..	..	..	..	..	..	4	3	7
21·5	..	..	..	..	..	..	..	..	..	..	2	2	4
22·0	..	..	..	..	..	..	..	..	..	..	..	1	1
22·5	..	..	..	..	..	..	..	..	..	..	..	2	2
Totals	97	111	147	70	17	2	100	200	213	60	54	26	1097
	444						653						

TABLE X. CALCULATED LENGTHS FROM OTOLITHS

At the end of	Calculated lengths in cm.: Male	Female
1st year	9·75	9·75
2nd year	13·25	14·75
3rd year	15·75	17·75
4th year	17·25	19·25

Growth rate from the Supra-Occipital Crest

The supra-occipital crest or spine is a thin flat piece of bone projecting from the posterior part of the skull like a triangular crest in the median line. The crest is made up of two parts, a frontal portion and a supra-occipital portion. The anterior frontal portion forms only a small part in the total crest. It starts

roughly in the anterior one-third of the frontal in the median line and rises from the skull at an angle of 45° (approx.). Immediately after passing the anterior one-third of the frontal, the crest bends back at an angle of 30° (approx.) to the plane of rise of the bone, and runs back to join the supra-occipital portion of the crest. The posterior edge of the frontal portion of the crest is split mesially, and the anterior edge of the supra-occipital portion of the crest is lodged in this split like the blade of a pen-knife when closed. It is a sort of interlocking joint which is more or less in the shape of an isosceles triangle. At the apex of this triangle, at the junction of the two portions of the crest, there is a slight depression of the border.

Method of Preparation

The method of collection of the supra-occipital was as follows. The fish was measured, its stomach removed and the sex determined. Then a small tape with the serial number of the fish written on it with chinese black ink or marking ink was pinned through its lower jaw and through the orbit on the opposite side. This enabled the pin to pass in between the roof of the skull and the palatine bridge and thus ensured the safety of the label in subsequent boiling. Brass safety pins were used as there was no chance of their rusting and corroding, and the same pins could be used over again for several samples. After the specimens had been labelled the heads were cut out behind the pectoral axil. These heads were then placed in a water-bath and cooked up to 80° C. The temperature at which the heads are cooked is a very important factor in the utilization of bones for age determination. If the heads are overcooked the bones assume an opaque consistency and their structure is blurred. It is always best to find out the optimum temperature for the cooking or, if that is not possible, to undercook rather than overcook. This is especially important when dealing with the heads of specimens of O- and I-year groups. After cooking, the flesh and other tissues from the skull were removed by washing the skull with a powerful jet of water. In that wet state all the bones are loose and disarticulated. The supra-occipital crest can be easily pulled out of the skull and it comes off with the supra-occipital bone attached to it like a narrow sloping base on either side of the crest. With sharp scissors this base of the supra-occipital bone was cut out from both sides of the base of the crest. The supra-occipital appears then as a clean, thin, flat piece of bone with no protuberances. The bone was then placed in a labelled envelope and exposed to the air on a wooden tray. It became dry in 24 hr. This is the best way of drying the bones. If the bones are dried in the heat of an electric bulb or over a warm plate, the zones become extraordinarily clear, but such artificial heat is apt to warp the bones in such a way as to interfere with the later measurements. When these bones are stored in the envelopes in a warm place the zones become quite clear and defined. The clarity of the zones increased with storage and drying. Rarely bones from

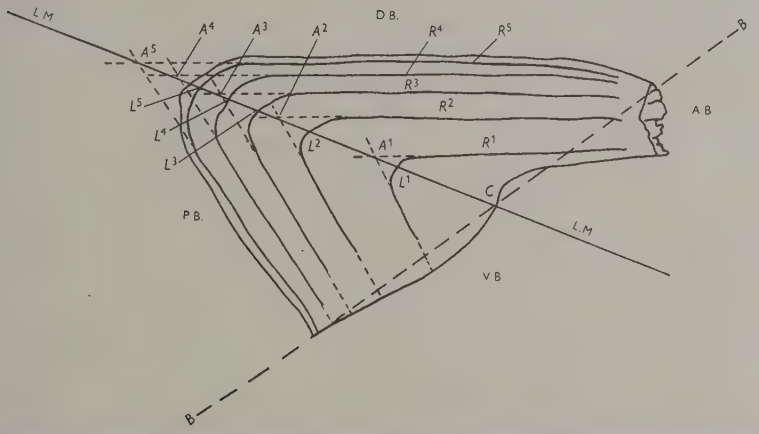
the older females contained a little fat. If this was not removed the bones took on a murky brown colour which blurred the zones to some extent during storage. The fat was removed by treatment with a mixture of equal amounts of benzene and ether, which yielded fine preparations within 24 hr. No difference was noticed in the nature and clarity of the zones due to refrigeration.

It is difficult to prepare the supra-occipital crests from formalin-preserved specimens. A few that had been collected in the early period of this work were washed in running water for 48 hr. and some of them were stained in alizarine according to the method of Tåning (1944). The other formalin-preserved heads were cut out behind the axil of the pectoral fins and boiled one by one in $2\frac{1}{2}\%$ caustic soda for about 5 min. With care and patience the supra-occipital spine could be removed from the skull, washed and air-dried. All these heads had to be cooked in boiling caustic soda or the bones of the skull never became disarticulated, and even then the results were not at all satisfactory. Usually, although the zones were quite clear, the bones showed the destructive effect of the caustic soda and were bent and curled. These bent bones did not give reliable measurements. As far as possible, therefore, a study of this type should be restricted to fresh or refrigerated specimens. If there is no choice and preserved specimens have to be dealt with, it is always best to use the alizarine-staining method. In the alizarine-stained specimens the opaque broad zones of the bone take a paler colour and rougher surface than the narrow transparent zones. Staining the bones with violet ink, indian ink and picro-carmine was tried. The inks stained the bones deeply and showed no differential shading in the staining. The picro-carmine staining was satisfactory only when the zones were clear and well defined. Dr Hart used violet ink for staining the vertebrae of *Phycis blennoides* and found it quite satisfactory (Menon, 1950). But he is of the opinion that staining is not at all necessary if the bones can be prepared from fresh material.

The supra-occipital crest of *Gadus minutus* shows on its surface broad bands of opaque, white zones alternating with thin, narrow and very transparent zones. The transparent bands appear like narrow lines to the naked eye. All these bands run more or less parallel to the edge of the crest. Each opaque zone gradually passes into the next transparent zone, but each transparent zone is very abruptly succeeded by the next opaque zone. This abrupt ending of a transparent zone and beginning of the next opaque zone is marked by a well-defined line. The innermost opaque zone of the crest is paler in colour and less opaque than the other opaque zones.

Each supra-occipital has four borders: an anterior border which enters into the interlocking joint with the frontal portion of the crest, an ascending dorsal border, a descending posterior border and a ventral border by means of which it joins with the supra-occipital bone in the skull. The ventral border is not straight but is bent at about the middle to form an anterior 'ascending half' and a 'posterior descending' half. The anterior border is comparatively very

small, so that the whole bone presents a triangular appearance with the base showing a median bend. Just behind the junction of the descending and ascending halves of the ventral border there is a point on the 'base-line' wherefrom arise several radiating lines and ridges which run towards the outer edge of the crest. In some bones these lines stand out as radiating rough ridges, but they do not interfere with the clarity of the zones or with the measurements. The posterior edge of the dorsal border is wavy or frilled in outline. This is the 'growing edge'. The point from which the radiating lines and ridges arise is the 'centre of growth' and the lines are the 'axes of growth' of the bone.



Text-fig. 6. Diagram of the theoretical projection of the rings into hypothetical triangles to fix the line of measurement on the supra-occipital crest. *B–B*, the hypothetical base-line; R^1 to R^6, the annual rings (outer limits of the transparent zones); *C*, the centre of measurements; A^1–A^5, the apical points of the hypothetical triangles; L^1–L^5, the points on the annual rings to which the measurements are made from the centre along the 'line of measurement' (L.M.). A.B., D.B., P.B., V.B., the anterior, dorsal, posterior, and ventral borders of the crest, respectively.

Line of Measurement

In utilizing a bone for the determination of age and rate of growth, the fixing of the line of measurement or axis of measurement is of prime importance. The line of measurement chosen for the supra-occipital crest is shown in Text-fig. 6. This axis of measurement was chosen because, apart from its convenience, (i) it is the median lying between the axis of vertical growth and the axis of horizontal growth of the fish and of the bone, and is therefore likely to give only the smallest error in calculations; and (ii) if all the zones are theoretically projected into hypothetical triangles this is the line which lies nearest to all the apical points and hence is to be regarded as the average of the sum forces of the axis of growth. In Text-fig. 6 it is shown how these

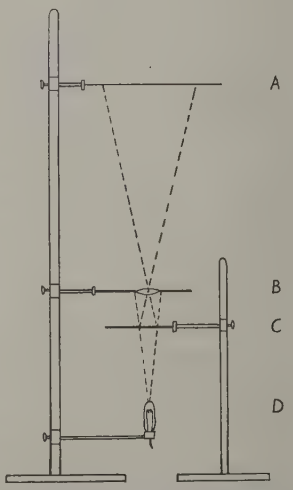
zones can be hypothetically projected into triangles. Since the anterior border of the crest is comparatively very small, the crest as a whole may be regarded as a triangle. The descending half of the ventral border is projected forward as a straight line meeting the anterior end of the dorsal border, and this forms the base-line of the triangle. Then the dorsal and posterior borders of the crest are projected in straight lines until they meet usually just behind the growing edge. This is the apex of the triangle. In the same way the dorsal and posterior borders of each of the transparent bands are projected to form hypothetical triangles. A line is drawn from the centre of growth passing along an axis which is nearest to the apical points of all the projected hypothetical triangles. This line is the line along which measurements were taken.

The diagram shows that the apical points lie almost in a straight line. This is because the growth of the bone is proportionate with the growth of the head and the allometry in the growth is altogether neglible.

Method of Measurement

The zones on the supra-occipital were measured by projecting the image of the crest on to graph paper covering a glass plate, with the aid of a simple vertical projector. The arrangement of the light, lens, the stage for the bone and the stage for holding the graph paper is shown in Text-fig. 7. A blue filter between the light and the bone increased the clarity of the image on the graph paper.

Quarto sheets of graph paper ruled in 10ths of an inch proved best for making the measurements. Each inch line is assumed as a separate ordinate and each such ordinate is used for a separate bone. The point of intersection between each such ordinate and the abscissa is taken to mark the centre of growth of the bone and the starting-point of the measurements. This point is superimposed on the centre of growth of the bone in the image. Fixing the graph paper at that point the paper is slightly rotated until the ordinate of that point lies in a line over the accepted axis of measurement of the bone in the image. The points at which each 'annual ring' (the sharp beginning of each opaque zone) in the image cuts the ordinate on the paper are then marked with a pencil. The posterior edge of the crest also is marked on the ordinate. The scale of magnification can be found by projecting a millimetre scale to the same



Text-fig. 7. Diagram of the simple vertical projector used for projecting the supra-occipital crests and for measuring them. *A*, stage for holding the graph paper and catching the image; *B*, the lens; *C*, stage for holding the bone; *D*, 6-watt lamp.

magnification on the graph paper. Knowing the magnification, the measurements of the zones on the graph paper can be easily converted into absolute measurements. When the various crests are all measured and marked on the graph paper, as described, it will be found that the respective annual-zone-points of the various crests lie more or less in a straight line. The crests were magnified to about eight times their normal size. With this magnification the percentage of error seems very small.

A few of the bones showed false rings—usually as 'split' or 'doubled' rings. These can be easily distinguished by the split not being continuous throughout the rings. The very few false rings where there was no 'doubling' could be distinguished by weak and incomplete formation, and by abrupt change from opaque to transparent zone, not gradual as with true rings. These were most easily detected in reflected light using a black background.

Validity of the annual nature of the zones

Graham (1929*b*), Sund (1927), Hickling (1933), Dannevig (1933) and Le Cren (1947) have all examined the validity of age-determination by scales, otoliths and bones respectively. Graham and Sund based their studies on the age-determination of cod on scales only, discarding the use of the skeletal parts because of the convincing evidence they got for the validity of the scale method. Hickling used only otoliths for the determination of the age of the hake and he had substantial evidence for its application and validity. The scales and otoliths of the Norwegian cod were critically studied by Dannevig (1933), and he came to the conclusion that 'the age of cod... certainly can be computed by scales and particularly by the otoliths'. The annual nature of the zones on the operculum of the Windermere perch was substantiated by Le Cren (1947).

According to Graham (1929*c*), there are five tests for deciding the validity of any method of age determination in fishes:

(i) Agreement with Petersen's method.
(ii) Seasonal record of the ring or zone formation.
(iii) Observation of a stock over a long period of years.
(iv) Marking experiments.
(v) Tank or pond experiments with fish of known age.

The present investigation of *G. minutus* covers only a period of 15 months and so it is not possible to examine the validity of the method of age determination employed from the aspect of test 3. Tests 4 and 5 were not possible for several reasons, and so it has been possible only to apply the remaining two tests to the validity of the present method.

Seasonal record

This test consists in the observation of the nature of the margin of the supra-occipital crest throughout the year, to find out and establish the period of formation of the opaque and transparent zones, and thus to determine

whether in the course of 1 year one opaque zone and one transparent zone only are laid. Graham (1929*a*) and Hickling (1933) remark that the seasonal record is a convincing test for the validity of the method. But neither of them found a sharp and complete turn over from one kind of marginal zone to the other at any time in the year. Hickling (1933) states: 'It is true that a sharp turn over from one margin to the other is completely lacking. No sample had 100% of its otoliths with an opaque zone at the edge and none had 0%.'

The percentages of supra-occipital crests of *G. minutus* with the opaque zones and transparent zones at the margin respectively for each month of the period of investigation are given in Table XI and in Text-fig. 8.

It can be seen from Table XI that in no month has there been a sample with 100% of the supra-occipital crests with either opaque zone or transparent zone at the margin. The maximum and minimum percentages of supra-occipital with the opaque and transparent zones have been 86 and 31, and 69 and 14 respectively. Hickling (1933) attributed the lack of complete turn over from one type of margin to the other in the otolith of the hake to the formation of 'subsidiary rings' in the growth of otolith as a normal feature. In the cod of Norwegian waters, on the other hand, Dannevig (1933) found a complete turn over from one type of margin to the other in both scales and otoliths. According to Hickling (1933) the causative factor for the ring formation in the otolith of the hake is an internal one and the nature of the zones depends on the condition of the fish and seasonal rate of growth of fish. Dannevig (1933) has suggested that the zone formation 'may be due to the variation in the quantity of organic substances'. The zones in the scales of cod, according to him, may 'originate in different ways by moderately low or very high temperature'.

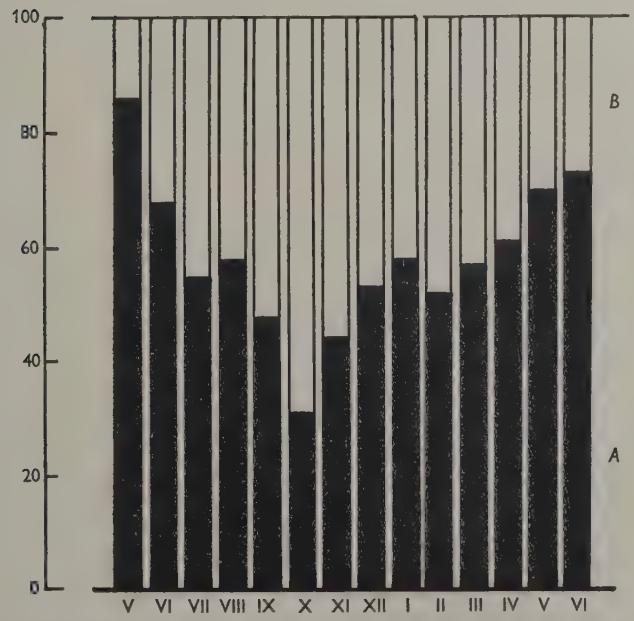
The data of the supra-occipital crests of *G. minutus* show that the percentage of these crests with an opaque zone at the margin remains fairly high from January to August. This percentage is low from September to November, the lowest being in the month of October. Hickling (1933) also got more or less identical results with the hake otolith. It was found that although there was no sharp turn over in the nature of the marginal zone at any particular period of the year, there were two distinct periods when the major emphasis was for the formation of one or the other type of zone. Thus the major period for laying the opaque zone is from January to August and that for the transparent zone is from September to November.

The results of the analysis of the margin of the supra-occipital crest are shown in Text-fig. 9. In addition two other factors, the condition factor K' for the fish in each month, and the average volume of food in the stomachs of ten fish in each month, have been included for comparison. The condition factor K used is the average for fish of all length groups and of both sexes together. Hickling (1933), in a similar study, treated the otolith data without taking sex into consideration and then compared it to the condition factor of

Table XI. Percentage of Fish with Opaque or Transparent Zones at the Margin of the Supra-Occipital Crest

The figures in brackets are the actual number of crests examined having the respective type of zone at the margin.

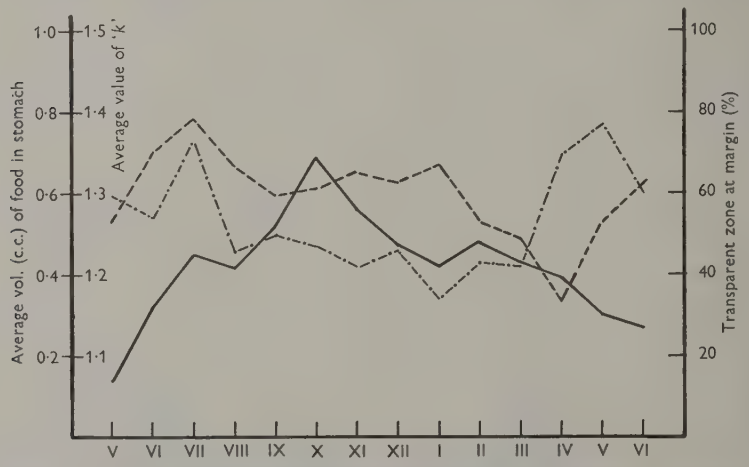
Month	Percentage of crests with opaque zone at the margin	Percentage of crests with transparent zone at the margin
May 1948	86 (68)	14 (11)
June	68 (76)	32 (36)
July	55 (34)	45 (28)
Aug.	58 (77)	42 (55)
Sept.	48 (67)	52 (72)
Oct.	31 (32)	69 (70)
Nov.	44 (51)	56 (66)
Dec.	53 (49)	47 (43)
Jan. 1949	58 (135)	42 (98)
Feb.	52 (117)	48 (110)
Mar.	57 (131)	43 (96)
Apr.	61 (92)	39 (59)
May	70 (111)	30 (47)
June	73 (51)	27 (19)



Text-fig. 8. Histogram showing the number of supra-occipitals per 100 examined exhibiting (*A*) the opaque zone, and (*B*) the transparent zone respectively at their margins in successive months.

the adolescent female hake. Although this did not lead to any conflicting results with the hake, it is better to treat such data from comparable factors and common standards when possible.

The condition factor is lowest during the spawning period February to May. This is the main period of formation of the opaque zone on the supra-occipital crests. Hickling (1933) found that 'the transluscent band is laid on the otolith of the hake at the time of the poorest condition, that is, of greatest physiological stress. In mature fish this is the exhaustion due to spawning and in immature fish to its precursor in the innate physiological rhythm which can be detected in the somatic tissues.' The observations on *G. minutus* show just



Text-fig. 9. The relation between condition, feeding, and zone formation in the supra-occipital of *G. minutus*. -·-·-·-, average volume in c.c. of food per stomach; ------, average '*K*' for the whole sample of fish; ——, the percentage of supra-occipital crests showing the transparent zone at the margin.

the reverse of this: the transparent zone is laid during a period of normal condition of fish (September to November) and the opaque zone is formed during the period of poorest condition of the fish (the spawning period). Yasuda (1940) made a similar observation on the otoliths and vertebrae of *Scombrops chilodipteroides* and *Theragra chalcogramma*. He observed that the rings on the otoliths and vertebrae are formed before spawning—3 months before spawning on the otolith and 1½ months before spawning on the vertebrae. It has been noticed that the spawning period in *Gadus minutus* is from February to May and the transparent zone (the counterpart of Yasuda's 'rings') is laid on the supra-occipital crest from September to November, i.e. the transparent zone is laid nearly 4–6 months after the spawning or, conversely, it is laid 2–4 months before the next spawning. If were are to accept

Hickling's (1933) finding that the fluctuation in the 'physiological stress' is the causative factor for the zone formation in the skeletal parts, it will have to be assumed that the effect of the physiological stress becomes apparent on the supra-occipital crest of *G. minutus* only some months after its actual occurrence.

Taking the average volume of food (Table I, p. 189) into consideration, we find that there is not much of a correlation with the zone formation. The highest percentage of supra-occipital crests with opaque zone at the margin is found during the period of 'most active feeding' and the lowest percentage of opaque-zone formation occurs during the period of 'average feeding'. But the correlation ends with this.

It appears that of these two factors—the physiological stress and feeding—the physiological stress is the more acceptable as the causative factor for the formation of the 'ring'. The effect of the physiological stress is made apparent on the bone as the transparent zone.

Without going further into the question on the causative factor, we find that the zones are annual, being laid at definite periods of the year and can be used as valid indices of age in *G. minutus*.

Agreement with Petersen's Method

This test is useful only if the following conditions are satisfied: (i) the sample analysed must be large; (ii) the samples must contain all the year groups in a proportion at least fairly comparable with their proportion in the population; (iii) the Petersen graph of the size analysis must show reasonably distinct modes.

Graham (1929*c*) has pointed out that the test is applicable to the first three or four age groups, and he further asserts that even in cases of agreement it only confirms the correctness of the method of age assessment for a fair majority of the fish.

Examining these three conditions of the utility of this test one notes that the first condition has no limiting factor. The bigger the sample, the closer is the approximation to the truth. There is no absolute criterion of the probable number in the sample to satisfy the condition. With regard to the third condition, only the modes of the early years will be distinct and well defined. As the rate of growth decreases with age the differences in the lengths of older age groups become very small and the Petersen curve tends to flatten at these later age groups. In fishes which have a short span of life this flattening of the curve may occur even earlier.

The second condition is especially important. The curve is one that represents the percentage composition of the length groups in a sample of population. The sample, therefore, should contain primarily all the year groups and, secondly, should contain them in such numbers that are proportionally comparable to their numbers in the population. In actual practice it is always possible that the gear employed for the collection of the samples

introduces a certain amount of selection in the sampling. In Text-figs. 10 and 11, showing the monthly analysis of the length groups of the *G. minutus* examined, the curve shows a very disturbing character, namely the absence of the O-group and I-group in the earlier samples. This is due to the selective

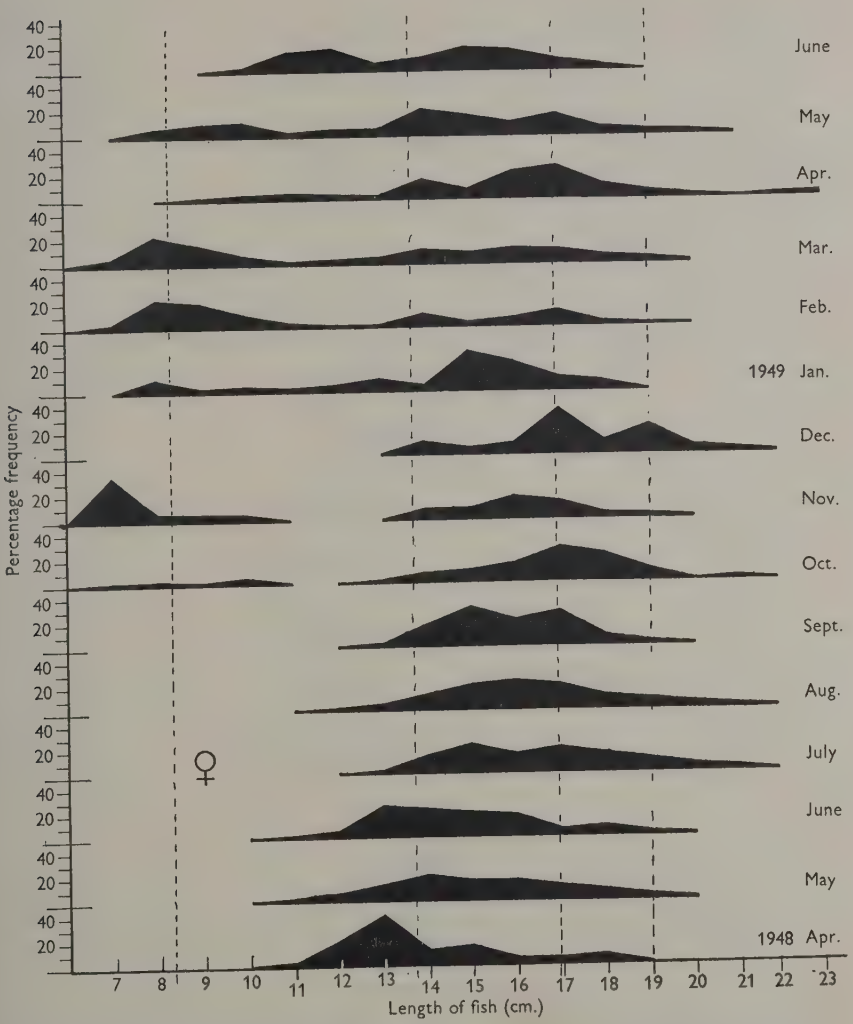
TABLE XII. TABLE SHOWING THE MONTHLY ANALYSIS OF THE SIZE OF THE SPECIMENS EXAMINED. FEMALE

Length of fish in cm.	1948									1949					
	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
7	..	..	..	..	..	..	1	96	..	..	13	6	..	..	..
8	..	..	..	..	..	..	2	18	..	9	89	35	..	14	..
9	..	..	..	..	..	..	1	15	..	3	77	24	1	19	..
10	..	..	..	..	..	..	7	14	..	4	41	9	8	24	6
11	2	6	4	..	..	..	..	..	..	2	11	1	11	6	29
12	3	14	11	..	2	..	..	..	..	5	2	3	8	9	33
13	21	29	74	6	13	2	4	..	..	9	3	6	5	9	11
14	45	47	70	30	34	34	14	22	14	4	38	14	33	49	17
15	13	42	57	49	53	60	16	22	6	29	12	12	16	33	33
16	15	43	51	32	59	42	25	47	11	23	28	18	48	19	30
17	5	25	13	42	55	53	46	38	49	11	36	17	63	37	14
18	4	17	20	29	31	13	39	9	15	7	11	8	25	12	8
19	6	4	4	18	22	5	16	6	31	..	6	6	10	7	..
20	..	..	..	8	11	..	..	..	6	..	3	..	2	4	..
21	..	..	..	3	3	..	1	..	4	..	..	..	..	..	..
22	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..
23	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..
	114	227	304	217	283	209	172	287	136	106	370	159	233	242	181

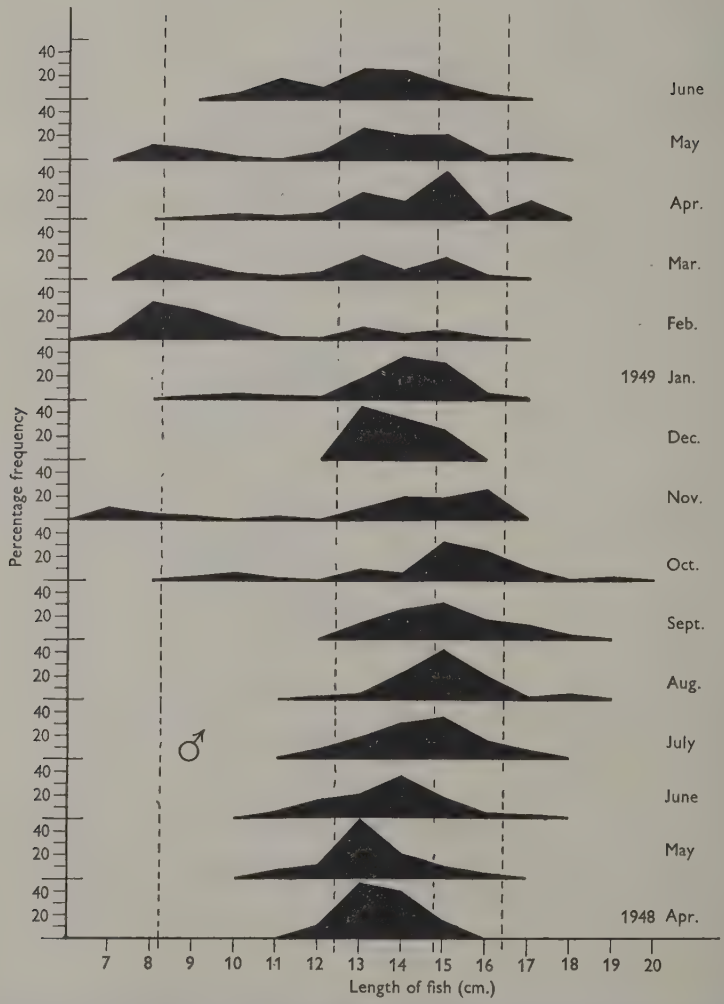
TABLE XIII. TABLE SHOWING THE MONTHLY ANALYSIS OF THE SIZE OF THE SPECIMENS EXAMINED. MALE

Length of fish in cm.	1948									1949					
	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
7	..	..	..	..	..	..	..	9	..	..	14	..	..	..	..
8	..	..	..	..	..	..	..	4	..	..	95	36	..	12	..
9	..	..	..	..	..	..	1	3	..	2	76	26	2	10	..
10	..	..	..	..	..	..	3	..	..	7	39	11	5	3	4
11	..	18	9	..	..	..	1	2	..	2	5	6	3	..	12
12	5	31	25	4	2	..	..	..	..	2	4	11	6	7	7
13	24	141	34	9	3	11	4	8	11	23	28	36	28	29	18
14	21	55	59	14	14	21	3	16	9	47	17	12	17	22	17
15	7	29	28	18	25	25	16	15	6	39	21	33	40	23	9
16	..	11	7	8	11	13	12	21	..	5	2	5	3	3	2
17	..	..	5	4	1	10	5	..	..	..	..	..	17	5	..
18	..	..	..	..	2	2	..	..	..	..	..	..	..	..	..
19	..	..	..	..	1	..	1	..	..	..	..	..	..	..	..
	57	285	167	57	59	82	46	78	26	127	301	176	121	114	69

sampling by the gear (Tables XII and XIII). Throughout the investigation the main gear used for the collection of the samples was the otter trawl, which would be liable to select against the smaller size groups. This is clearly seen in the earlier part of the investigation in which the O-group was completely lacking. Later it was possible to collect a few of the O-group specimens from



Text-fig. 10. The size-composition (length-frequency) of the females in the samples of *G. minutus* in successive months. ------, the yearly lengths back-calculated from the supra-occipital crests.



Text-fig. 11. The size-composition (length-frequency) of the males in the samples of *G. minutus* in successive months. ------, the yearly lengths back-calculated from the supra-occipital crests.

the trawling surveys of Mr P. G. Corbin, who used the ordinary otter trawl with a sprat-net cod-end. All these have been included in the graphs. Also plotted on the graphs are the lengths that the fish reaches at the end of each year calculated from the supra-occipital. These are shown as vertical lines at the respective 'calculated lengths'. The spawning period of the fish is from February to May with its maximum in April. It can then be assumed that this period is the initial starting-point of the annual growth. It can be seen from the graphs that the first mode of the curves in the graphs for January, February and March in the female, and February, March and May in the male, lie more or less on the calculated lengths. In November 1948, another month when some specimens of O- and I-groups were obtained, the first mode lies much in front of the calculated length for the first year. The 2nd year and 3rd year modes also show more or less the same position as the calculated lengths in the months of February, March, April and May in the size-analysis graphs for both male and female. It is not possible to follow one lower-age

TABLE XIV

	Male		Female	
At the end of	Mode or observed length in cm.	Calculated length in cm. (from supra-occipital)	Mode or observed length in cm.	Calculated length in cm. (from supra-occipital)
1st year	8	8·2	8	8·3
2nd year	13	12·4	14	13·7
3rd year	15	14·8	17	16·9

class throughout the year in the graphs due to the influence of selective sampling by the gear. But the close approximation of the first three modes to the calculated lengths for the first 3 years in the months of February to May, in general, is a fair vindication of the test and the validity of the method (see Table XIV). Considering that the modes are given only to the nearest cm. the agreement is as exact as can be expected.

AGE AND RATE OF GROWTH OF *GADUS MINUTUS*

The above two tests have substantially confirmed that the zones are annual and one opaque zone and its immediately succeeding transparent zone denote 1 year's growth and that they are the 'annual rings' comparable to the annual rings of the scales and otoliths of other fishes.

The mean lengths of the supra-occipital crest at each 5 mm. body-length in the male and female respectively are given in Table XV and plotted in Text-figs. 12 and 13 against the respective body-lengths as correlation curves.

The mean lengths of the 1st, 2nd, 3rd rings, etc., at each respective body-length, have been included in the graphs to represent the respective rings on the length-group of the supra-occipital. It can be seen from this that the lengths of each annual ring lie along a straight line, to quite a remarkable

degree, clearly proving that the rings once formed did not show any addition or diminution in their sizes and quality. The back-calculation was done in two ways—graphically and by the Lea-Dahl formula. The graphical back-calculation was carried out as follows.

TABLE XV. TABLE SHOWING THE LENGTH OF THE SUPRA-OCCIPITAL CREST AT THE DIFFERENT LENGTHS OF FISH

	Length of the supra-occipital crest in mm.					
	Female			Male		
Length of fish in cm.	Empirical mean lengths	S.E. of mean	Theoretical lengths X	Empirical mean lengths	S.E. of mean	Theoretical lengths Y
7·0	2·81	0·029	2·69	2·78	0·033	2·69
7·5	3·07	0·033	2·97	2·99	0·024	2·97
8·0	3·38	0·031	3·24	3·32	0·028	3·24
8·5	3·60	0·034	3·52	3·44	0·017	3·52
9·0	3·83	0·026	3·71	3·72	0·033	3·79
9·5	3·99	0·033	4·03	3·98	0·038	4·07
10·0	4·41	0·033	4·34	4·36	0·037	4·34
10·5	4·79	0·020	4·66	4·57	0·035	4·62
11·0	4·96	0·039	4·98	5·01	0·026	4·89
11·5	5·21	0·030	5·30	5·21	0·025	5·16
12·0	5·58	0·030	5·62	5·42	0·035	5·44
12·5	5·92	0·047	5·94	5·62	0·038	5·71
13·0	6·32	0·031	6·25	6·04	0·032	5·99
13·5	6·60	0·039	6·57	6·30	0·035	6·26
14·0	6·81	0·083	6·89	6·68	0·042	6·54
14·5	7·12	0·052	7·21	6·85	0·035	6·81
15·0	7·56	0·052	7·53	7·10	0·038	7·09
15·5	7·85	0·058	7·85	7·54	0·039	7·36
16·0	8·16	0·035	8·17	7·71	0·045	7·64
16·5	8·66	0·049	8·48	8·08	0·052	7·91
17·0	8·86	0·056	8·80	8·32	0·029	8·19
17·5	9·07	0·082	9·12	8·45	0·039	8·46
18·0	9·45	0·082	9·44	8·69	0·021	8·74
18·5	9·87	0·074	9·76	(8·88)	..	9·01
19·0	10·24	0·071	10·08	..	..	..
19·5	10·37	0·046	10·39	..	..	..
20·0	10·69	0·064	10·71	..	..	..
20·5	11·13	0·048	11·03	..	..	..
21·0	11·40	0·058	11·35	..	..	..
21·5	11·60	0·067	11·67	..	..	..
22·0	(11·96)	..	11·99	..	..	..
22·5	(12·26)	0·010	12·30	..	..	..

Notes. X, Y; the theoretical lengths calculated from the formulae:

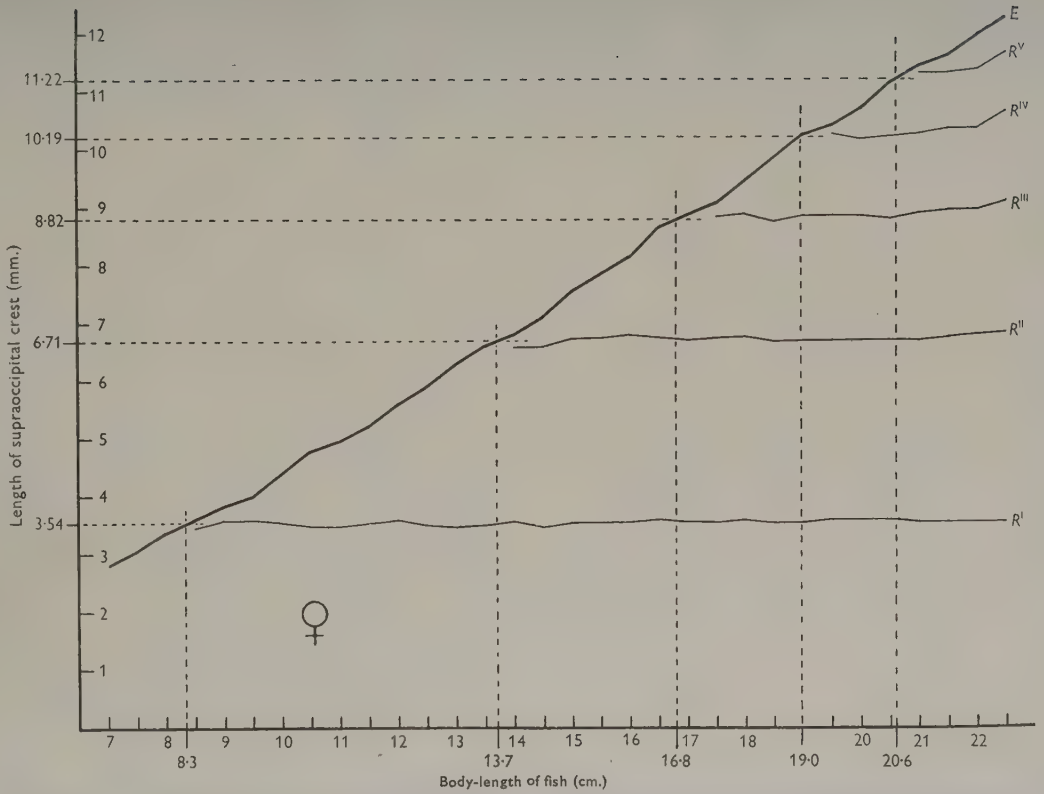
$L = 3{\cdot}18 + 1{\cdot}57l$ for the females above 9·0 cm.,

and $L = 2{\cdot}10 + 1{\cdot}82l$, for the males.

The theoretical lengths for the groups below 9·0 cm. in the females were calculated from the formulae used for the males. The empirical lengths are nearly the same in both sexes towards the lower length groups. The difference in the lengths of the supra-occipital crests in the two sexes is marked from maturity.

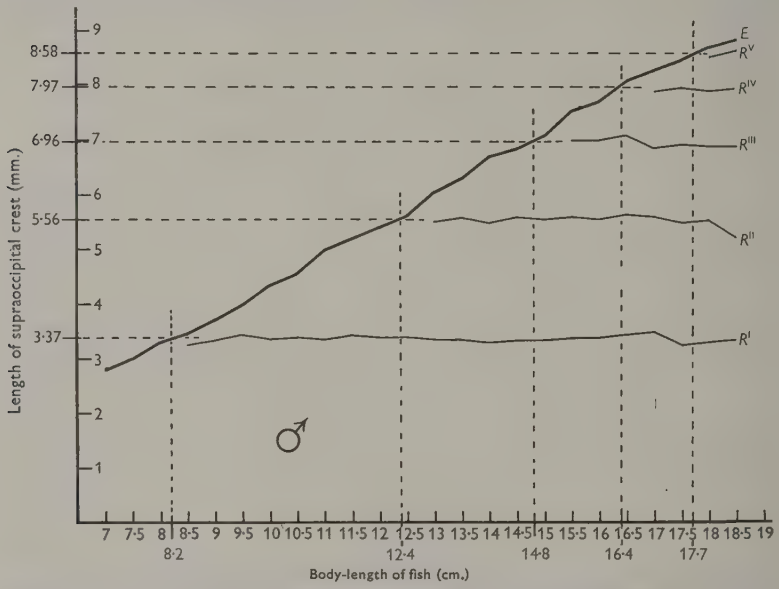
The figures in brackets denote that the number of crests examined were less than 5.

The mean lengths of the 1st, 2nd, 3rd, 4th and 5th 'rings' were worked out from all the supra-occipitals examined for either sex irrespective of the lengths of the fish (Table XVI).



Text-fig. 12. The relation between the body-length of fish and length of supra-occipital crests in the female *G. minutus*. The curve *E* is the length of crest from the centre of measurements to the growing edge. Curves R^I to R^V are the mean lengths of the respective annual rings on the crest at different body-lengths.

These lengths were then plotted on the abscissa of the graph of the curve of correlation of the length of fish and length of supra-occipital crests. They were then projected straight to cut the correlation curve. The points at which



Text-fig. 13. The relation between the body-length and length of supra-occipital crest in the male *G. minutus*. The curve *E* is the length of crest from the centre of measurement to the growing edge. Curves R^{I} to R^{V} are the mean lengths of the respective annual rings on the crest at different body-lengths.

TABLE XVI. MEAN LENGTHS (IN MM.) OF SUCCESSIVE ANNUAL RINGS

	Female			Male		
	Mean length	S.D.	S.E. of the mean	Mean length	S.D.	S.E. of the mean
I ring	3·54	0·31	0·01	3·37	0·27	0·01
II ring	6·71	0·24	0·01	5·56	0·21	0·01
III ring	8·82	0·27	0·02	6·96	0·23	0·02
IV ring	10·19	0·29	0·04	7·97	0·17	0·03
V ring	11·22	0·14	0·04	8·58	0·21	0·11

these lines cut the curves were then projected vertically down to meet the ordinate containing the body-lengths. The points at which these vertical projections cut the ordinate denoted the 'calculated lengths' of the fish at the end of the 1st, 2nd, 3rd, 4th and 5th years respectively. The calculated lengths thus arrived at are given in Table XVII.

The actual observations from the supra-occipital crests show slightly higher values for the body-lengths. The various 5 mm. length groups of either sex are tabulated below according to the number of 'annual rings' or age discerned on their respective supra-occipital crests as with the scales and otoliths (Table XVIII).

TABLE XVII. 'CALCULATED LENGTHS', DERIVED FROM MEASUREMENTS OF THE SUPRA-OCCIPITAL CREST

At the end of	Body-length of fish in cm.	
	Female	Male
1st year	8·3	8·2
2nd year	13·7	12·4
3rd year	16·9	14·8
4th year	19·0	16·4
5th year	*c.* 20·6	*c.* 17·7

TABLE XVIII. ANALYSIS OF THE SUPRA-OCCIPITAL CRESTS OF *GADUS MINUTUS* ACCORDING TO THE LENGTH AND AGE OF THE FISH

Length of fish in cm.	Age in years: Female						Male						Total
	1−	1+	2+	3+	4+	5+	1−	1+	2+	3+	4+	5+	
7·0	20	..	..	..	..	..	11	..	..	..	..	..	31
7·5	36	..	..	..	..	..	10	..	..	..	..	..	46
8·0	34	9	..	..	..	..	36	1	..	..	..	..	80
8·5	24	18	..	..	..	..	23	19	..	..	..	..	84
9·0	12	22	..	..	..	..	15	26	..	..	..	..	75
9·5	6	34	..	..	..	..	..	32	..	..	..	..	72
10·0	..	50	..	..	..	..	..	20	..	..	..	..	70
10·5	..	31	..	..	..	..	..	19	..	..	..	..	50
11·0	..	35	..	..	..	..	..	32	..	..	..	..	67
11·5	..	38	..	..	..	..	..	34	..	..	..	..	72
12·0	..	26	..	..	..	..	..	30	..	..	..	..	56
12·5	..	35	..	..	..	..	..	33	8	..	..	..	76
13·0	..	40	..	..	..	..	..	11	50	..	..	..	101
13·5	..	24	9	..	..	..	..	4	58	..	..	..	95
14·0	..	20	16	..	..	..	..	..	65	2	..	..	103
14·5	..	16	26	..	..	..	..	..	65	9	..	..	116
15·0	..	4	54	..	..	..	..	..	42	19	..	..	119
15·5	..	1	57	..	..	..	..	..	3	56	2	..	119
16·0	..	..	74	1	..	..	..	..	..	14	7	..	96
16·5	..	..	54	5	..	..	..	..	..	9	9	..	77
17·0	..	..	40	11	..	..	..	..	..	..	9	..	60
17·5	..	..	14	22	..	..	..	..	..	..	2	2	40
18·0	..	..	4	29	..	..	..	..	..	..	1	1	35
18·5	..	..	..	22	4	..	..	..	..	..	..	1	27
19·0	..	..	..	14	5	..	..	..	..	..	..	..	19
19·5	..	..	..	7	11	..	..	..	..	..	..	..	18
20·0	..	..	..	..	11	..	..	..	..	..	..	..	11
20·5	..	..	..	..	10	..	..	..	..	..	..	..	10
21·0	..	..	..	..	2	5	..	..	..	..	..	..	7
21·5	..	..	..	..	1	3	..	..	..	..	..	..	4
22·0	..	..	..	..	..	1	..	..	..	..	..	..	1
22·5	..	..	..	..	..	2	..	..	..	..	..	..	2
Total	132	403	348	111	44	11	95	261	291	109	30	4	1839

From this table the means of lengths arrived at the end of each year were calculated as with the data of scales and otoliths. These mean lengths are the 'observed lengths' (Table XIX).

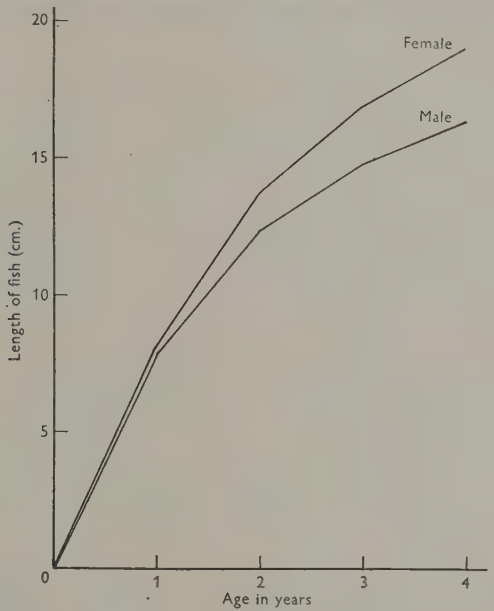
Table XIX. 'Observed Lengths', Derived from Grouping the Fish According to the Number of Annual Rings in the Crest

At the end of year	Length of fish in cm.			
	Female		Male	
	Range	Mean	Range	Mean
1st	8·5–9·0	8·75	8·5–9·0	8·75
2nd	14·0–14·5	14·25	12·5–13·0	12·75
3rd	17·0–17·5	17·25	15·0–15·5	15·25
4th	19·0–19·5	19·25	16·0–16·5	16·25

Working out these means as with otoliths and scales, it is found that the differences between the graphically calculated lengths and the 'observed mean lengths' diminish with age.

The growth of *G. minutus* diminishes with age. The maximum size to which the fish usually grows is about 22·5 cm. in the female and 19·0 cm. in the male. The maximum age to which the fish generally lives is found to be 5 years. Only four males and eleven females of over 5 years' age have been seen, and so the measurements of their supra-occipital crests give only rough and approximate averages. Because of this the length that the fish reaches at the end of its 5th year, calculated from the measurements of the crest, is not included in Table XXI. The calculated lengths of the fish at the end of each year have been plotted in Text-fig. 14. It is seen from this that the rate of growth is extremely rapid in the first year. In the 2nd and 3rd years the growth diminishes, and it is very little from the 4th year onwards. The sexes grow at different rates. This is a well known feature in several other fishes, the males growing more slowly than the females. Comparing the growth rate of males with that of the females it is seen that both grow at the same rate and pace in the first year reaching almost the same lengths, viz. 8·2 and 8·3 cm. respectively. Maturity is reached at the beginning of the 2nd year and spawning occurs for the first time in the 2nd year of life. The males grow slower than the females in this 2nd year but the difference in growth is not very marked, the final lengths at the end of the 2nd year being 13·7 cm. in the female and 12·4 cm. in the male. After the spawning the differential growth between the male and the female becomes very marked. Hickling (1933), in *Merluccius merluccius*, and Hart (1946), in *Merluccius hubbsi*, have pointed out that the metabolic strain of spawning is greater in mature males than in females. Greater energy is spent in building up the reserves of the reproductive elements than in linear growth in a spent male. This is a very likely cause for the difference in growth rate between the males and females of *Gadus minutus* after the first spawning in the 2nd year. The diminution in the rate of growth of females

after the first spawning is also marked, but not to the same extent as in the males. With every succeeding year the growth rate diminishes at such a rate that the males reach the same length in 4 years as the females reach in 3 years.



Text-fig. 14. Average growth rate of the male and female *G. minutus*.

The respective annual increments for each of the first 4 years of life in the male and the female are shown in Table XX.

It is significant that while the growth of females in each year is approximately two-thirds that of the preceding year, the growth in the male is approximately only half that of the preceding year.

TABLE XX. ANNUAL GROWTH INCREMENTS (CM.) DERIVED FROM 'CALCULATED LENGTHS'

Year	Female	Male
1st	8·3	8·2
2nd	5·4	4·2
3rd	3·2	2·4
4th	2·0	1·6

The comparatively much smaller number of males over 5 year's age in the population analysed can only be due to the reason suggested by Hickling (1933) for the hake. 'In the male hake, it is certainly true that the metabolic strain of the reproduction cycle increases at a very high rate with increase of length and there is no evidence that the male can prolong its life by a slackening off

of sexual activity.' The facts point rather towards a condition when 'reproduction may eventually overbalance normal metabolism and result in death' (Orton, 1929). The maturity at the beginning of the 2nd year, the occurrence of spawning in the 2nd spring of its life and the consequent differential metabolic strain can well be regarded as the primary factors influencing the differential growth rate in the two sexes in *G. minutus*.

Growth in Length of the Supra-Occipital Crest

The relation between the length of the supra-occipital crest and the length of the fish is important in the application of the Lea-Dahl formula for back-calculation. The mean lengths of the supra-occipital crests at the different lengths of fish plotted in Text-figs. 12 and 13 show that all the points in each sex lie more or less in a straight line at all body-lengths above 7·0 cm. in the male and 9·0 cm. in the female. This direct relation of the length of the fish to the length of the supra-occipital can be expressed by the formula

$$L = a + bl,$$

where L is the length of fish in cm., l is the length of the supra-occipital crest in mm., and a and b are constants, b representing the ratio of increments of length of body and supra-occipital crest.

The lengths of the supra-occipital crests of the male are slightly lower than those of the female at corresponding body lengths and so the constants a and b are not the same in the two sexes, at least from the time they are beginning to mature. In each of the graphs (Text-figs. 12 and 13) the constants are obtained from the best-fitting straight line, a being given by the value of L when l is zero, and b being the ratio given by the slope of the line (the tangent of its angle to the vertical).

Interpolating the values of the constants in the formula for *G. minutus*, it becomes

$L = 3{\cdot}18 + 1{\cdot}57l$ for the female above 9·0 cm.,
and $L = 2{\cdot}10 + 1{\cdot}82l$ for the male (and probably all immatures).

Using these formulae it is possible to back-calculate the lengths of fish at any particular length of the supra-occipital crest. Conversely the theoretical lengths of the supra-occipital crests at any particular body-length also can be calculated. The theoretical lengths of the supra-occipital crests calculated by means of these formulae are given in Table XV (p. 220).

It is found that the back-calculated lengths of fish estimated by these formulae differ from the actual observed lengths only by 0·1–0·5 cm.

It would appear from the formula $L = a + bl$ that the value of 'a' is the length of fish at which the supra-occipital crest begins to develop. If so the crest ought to develop at 2·1 cm. But actually the supra-occipital crest is first observed when the fish is 1·1 cm. long (it appears as a very narrow and small streak on the dorsal aspect of the neurocranium). If this 'presupraoccipital

fish length' of 1·1 cm. is applied to the orthodox Lea-Dahl formula it is possible to back-calculate body-lengths from the formula

$$L_r = \frac{L_R}{l_R} l_r + 1{\cdot}1,$$

where L_r and L_R are two different body-lengths, with l_r and l_R their corresponding crest-lengths. The ratio L_R/l_R has been found empirically, l_r is any chosen crest-length, and L_r the body-length which is to be calculated. The modified Lea-Dahl formula differs from that used above (viz. $L = a + bl$) in having a smaller value for 'a' and in using an empirical ratio which tends to be greater than 'b'. The lengths back-calculated by the modified Lea-Dahl formula usually differ from the actual observed lengths by 0·1 to 0·9 cm., and, except for the smallest immature fish, the formula seems to have no particular merit.

Comparison between the Growth Rate Determined by Supra-Occipital Crest, Scales, Otoliths and Petersen Method

The length of the fish at the end of the respective years of its life history arrived at by examination of the scales, otoliths, supra-occipital crests and the size analysis are now compared (Table XXI). The data of the lengths calculated from the supra-occipital crests are given in two ways—one showing the lengths calculated by the graphical method, and the other calculated by the Lea-Dahl formula.

TABLE XXI. CALCULATED LENGTHS IN CM. OF *GADUS MINUTUS*

Age (years)	From scales	From otoliths	From supra-occipital		From size analysis
			Graphical	L–D formula	
		Female			
1	8·75	9·75	8·3	7·7	8·0
2	14·25	14·75	13·7	13·5	14·0
3	17·25	17·75	16·9	17·4	17·0
4	19·75	19·25	19·0	19·0	..
		Male			
1	8·75	9·75	8·2	8·0	8·0
2	12·75	13·25	12·4	12·5	13·0
3	15·25	15·75	14·8	15·4	15·0
4	16·75	17·25	16·4	16·4	..

In the back-calculation by the Lea-Dahl formula all the lengths have been calculated from the fish length and supra-occipital length of the fish at the end of the 4th year. All these lengths are standard lengths. The values arrived at by using the supra-occipital measurements are nearest to the actual observed lengths found in the size analysis. The lengths derived by examination of the otoliths and scales are higher than the empirical lengths. The differences between the lengths calculated by the graphical method and those by the Lea-Dahl formula are only 0·2–0·6 cm., which are unimportant in adults.

These calculated lengths and the age and growth rate of female *G. minutus* calculated from supra-occipital crests compare quite well with the findings of Stuart Thomson (1904), allowing for certain personal errors. Cunningham (1891) made some interesting observations on the growth rate of *G. minutus* by size analysis. The measurements and other details given by him are quoted in Table XXII.

Cunningham states that the more than 200 specimens less than 3 in. in length collected from Whitsand Bay 'are undoubtedly from the ova shed the preceding spring.... It is also clear that the specimens of 4·5–6·4 in. obtained on 9 July 1891 near the Eddystone were in their second year.' As growth rate decreases gradually, he regarded specimens of April 1891 to be 2 years of age.

Table XXII. Summary of Cunningham's Observations on *Gadus minutus*

Date	Length in cm.	Length in in.	Calculated age	Place of capture
May 1890	2·8–4·3	1·1–1·7	8–12 weeks	Cattewater
June 1891	4·2–7·2	1·6–2·9	About 3 months	Whitsand Bay
July 1891	11·5–16·2	4·5–6·4	1 year and 3 months	North of Eddystone
April 1891	14·3–19·0	5·6–7·5	2 years	East of Eddystone
June 1889	13·7–15·0	5·4–5·8	1 year and 2 months	Whitsand Bay
	20·0	7·8	2 years and 2 months	Whitsand Bay

Cunningham's estimation of the length reached in the 1st year coincides fairly well with the present findings. His consideration of the 14·3–20 cm. length-group as belonging to one and the same age group, viz. past 2 years, is incorrect. That length group is really composed of two or even three age classes. The treatment of the data irrespective of sex also has contributed to the mixing of the different year classes.

The Relation Between the Length and Weight of *Gadus minutus* and its Value as an Index of the Spawning Season

Hickling (1930, 1940) and Hart (1946) have shown how the analysis of the weights of fish may yield interesting results from which important conclusions can be drawn. All the *G. minutus* were weighed in a Salter spring balance to the nearest gram. These weights were treated separately for each cm. length group and month in either sex. From the weights of several specimens of a cm. length group, the average weight for that particular length group was worked for each month. These average weights were used for computing the ponderal index for separate cm. length-groups of either sex. The ponderal index was worked out from the formula used both by Hickling (1930) and Hart (1946), viz.:

$$K = \frac{W}{L^3} \times 100,$$

where W is the average weight of fish in gm., L is the mean length of fish in cm. and K is the ponderal index to be calculated. With suitable precautions

the ponderal index can often be taken as a measure of the fish's condition, and in these circumstances can appropriately be termed 'condition factor'.

Ponderal indices have been computed in three ways:

(i) Ponderal index for each mean cm. length group for each month in either sex.

(ii) The average ponderal index for each cm. length group of either sex for the whole year.

(iii) The average ponderal index of the whole sample of fish of either sex in every month.

Hart (1946) has stated that the *K* values may give a very good idea of the broad outline of the seasonal cycle for the species. He observed that 'apart from the seasonal variation in condition there is a secondary variation related to the length of the fish'. With increase in age 'there is a lower level of condition throughout the seasonal cycle consequent upon the increased metabolic strain of spawning. The point of inflexion on a curve showing this diminution of *K* with increasing length is thus a good indication of the length at which sexual maturity is attained.' In a growing organism a progressive variation of the ponderal index can be due to allometric growth. This point has been borne in mind when using the ponderal index variation of the *G. minutus* as an indicator of the spawning period.

The average values of *K* in relation to the length of the fish of either sex are given below (Table XXIII).

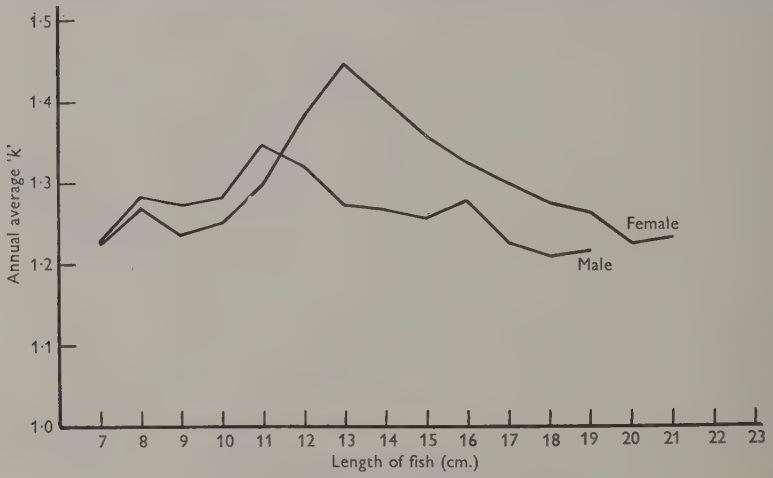
TABLE XXIII

Mean length of fish in cm.	Female		Male	
	No. of specimens	*K*	No. of specimens	*K*
7	116	1·224	23	1·224
8	167	1·270	147	1·282
9	140	1·235	120	1·271
10	113	1·250	72	1·280
11	72	1·297	58	1·347
12	90	1·383	104	1·320
13	192	1·448	407	1·272
14	465	1·402	344	1·266
15	453	1·356	334	1·253
16	491	1·322	103	1·275
17	504	1·299	47	1·225
18	248	1·273	4	1·209
19	141	1·263	2	1·214
20	34	1·224	..	..
21	11	1·231	..	..
22	1	1·018	..	..
23	2	0·789	..	..

These average values of *K* in relation to the length of fish of either sex have been plotted as two curves in Text-fig. 15.

From the above graph it is seen that the *K* value is low in the very small length groups and gradually builds up until it falls in the greater length groups. If the point of inflexion of these curves is to be taken as an index of the length

at first spawning, it is found that the males mature at an average length of 11 cm. and the females at an average length of 13 cm. The *K* values of males are higher than those of the females of corresponding lengths before maturity. The *K* values of mature and post-mature males are lower than those of the females of corresponding lengths. This agrees with the observations of Hickling (1930) on the European hake and Hart (1946) on the Patagonian hake. These low values of *K* for the mature and post-mature males have been explained by Hickling (1930) as due to 'the very rapidly increasing metabolic strain of spawning in the older males'. From direct observation it has been



Text-fig. 15. The average *K* at the different lengths of fish in the male and female *G. minutus*.

noticed that the majority of males below 11 cm. and the majority of females below 13 cm. are immature; but observations on the actual gonadial changes could not be carried out in detail. In general, however, the deduction seems fairly substantiated that the average male matures at 11 cm. and the average female at 13 cm. Maturity is thus attained when the fish is in its 2nd year of life. The early maturity in contrast to the long adolescence of so many other larger gadoids is presumably due to the shorter span of life of *G. minutus*.

The length at which the fish matures now having been fixed, data from the *K* values have been selected to examine the seasonal variation of the ponderal index of each length group of either sex. These monthly variations of *K* are given in Table XXIV.

The variation of *K* values indicates the spawning period of the fish. The decline in the values denotes the beginning of the spawning in the species, since this downward trend is assumed to be consequent upon the lower level

Table XXIV. Table Showing the Ponderal Index *K* for the Individual Length Groups in the Different Months

Year	Month	Length in cm. 7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
								Female										
1948	May	..	..	..	..	1·248	1·393	1·488	1·185	1·233	1·221	1·079	1·235	1·283	..	..	..	..
	June	..	..	..	..	1·254	1·410	1·639	1·294	1·252	1·367	1·303	1·235	1·370	..	..	..	..
	July	..	..	..	..	..	..	1·684	1·603	1·511	1·489	1·434	1·285	1·312	1·188	(1·296)	..	..
	Aug.	..	..	..	..	..	(1·447)	1·442	1·567	1·481	1·318	1·425	1·344	1·283	1·338	(1·339)	..	..
	Sept.	..	..	..	..	..	..	(1·431)	1·385	1·363	1·294	1·303	1·372	1·312	..	..	..	..
	Oct.	(1·268)	(1·290)	(1·235)	1·264	..	..	1·468	1·585	1·463	1·416	1·343	1·269	1·327	..	(1·080)	..	..
	Nov.	1·215	1·272	1·255	1·281	..	..	..	1·603	1·523	1·440	1·323	1·235	1·356	..	..	..	..
	Dec.	..	..	..	..	..	..	..	1·541	1·492	1·416	1·364	1·252	1·254	1·188	1·209	..	..
1949	Jan.	..	1·276	(1·246)	1·241	(1·325)	1·331	1·488	1·505	1·514	1·392	1·364	1·372	..	..	..	..	..
	Feb.	1·189	1·260	1·221	1·231	1·254	(1·403)	(1·332)	1·348	1·314	1·270	1·312	1·303	1·196	(1·325)	..	..	..
	Mar.	..	1·242	1·214	1·224	(1·251)	(1·331)	1·304	1·276	1·185	1·270	1·282	1·303	1·166	..	..	..	..
	Apr.	..	..	(1·239)	1·259	1·251	1·373	1·304	1·130	1·126	1·118	1·229	1·143	1·101	(1·125)	..	(1·018)	(0·789)
	May	..	1·246	1·224	1·234	1·387	1·366	1·370	1·228	1·252	1·200	1·131	1·212	1·196	1·180	..	..	..
	June	..	1·294	1·246	1·266	1·341	1·392	1·424	1·284	1·272	1·298	1·222	1·262	..	..	..	..	..
								Male										
1948	May	..	..	..	..	1·297	1·331	1·286	1·276	1·221	1·221	..	..	..				
	June	..	..	..	..	1·317	1·465	1·350	1·309	1·294	1·468	1·291	..	..				
	July	..	..	..	..	..	1·401	1·314	1·312	1·310	1·492	1·253	..	..				
	Aug.	..	..	..	..	..	(1·331)	(1·261)	1·290	1·271	1·221	(1·221)	(1·217)	(1·218)				
	Sept.	..	..	..	..	..	..	1·257	1·265	1·256	1·231	1·214	(1·200)	..				
	Oct.	..	..	(1·254)	(1·270)	(1·372)	..	1·268	(1·276)	1·268	1·251	1·221	..	(1·210)				
	Nov.	1·332	1·291	(1·282)	..	(1·380)	..	1·261	1·285	1·276	1·258	..	..	..				
	Dec.	..	..	..	..	..	..	1·272	1·271	1·288	..	..	..	..				
1949	Jan.	..	..	(1·242)	1·290	(1·325)	(1·242)	1·264	1·284	1·299	1·371	..	..	..				
	Feb.	1·116	1·242	1·235	1·280	1·360	1·231	1·239	1·221	1·215	(1·201)	..	..	..				
	Mar.	..	1·264	1·228	1·290	1·346	1·209	1·214	1·203	1·165	1·170	..	..	..				
	Apr.	..	..	(1·212)	1·224	(1·209)	1·199	1·163	1·186	1·156	(1·147)	1·118	..	..				
	May	..	1·329	1·317	(1·292)	..	1·339	1·292	1·260	1·240	(1·228)	1·261	..	..				
	June	..	..	..	1·302	1·368	1·435	1·312	1·286	1·283	(1·314)	..	..	..				

The numbers of individuals on which the above figures are based may be ascertained from Tables XII and XIII.
The figures in brackets are based on 3 or less than 3 individuals.

of condition 'due to the increased metabolic strain'. The decline occurs after January and the mean K values remain low till May. This indicates that the spawning period of the fish is between February and May. The lowest level of condition is in March–April when the spawning is at its height. This observation agrees well with Cunningham's (1891) assumption, in his computation of the growth rate of the fish, that the annual life cycle of *G. minutus* begins in April. In June and July there is a rapid recovery and increase of K in both sexes. There is a minor drop in August and September, but this drop is much smaller than that observed during the spawning months. In the analysis of the food of *G. minutus* three periods had been distinguished in the annual life cycle of the fish according to their feeding activity; viz. a period of low feeding synchronizing with the months of spawning, a period of active feeding during the months immediately following the spawning, when the fish is recuperating from the strain of spawning, and a period of 'average feeding' when the fish is growing. During the period of low feeding the K value is very low, and during the period of active feeding there is a sudden increase in the K values. The K values show a fluctuation during the period of average feeding when the fish is growing. At the beginning of this period, i.e. in August and September, there is a minor drop in the condition factor. It is possible that the metabolic changes in the fish at this period tend more towards an increase in linear dimensions than the building up of weight, a process which would automatically reduce the condition factor.

There is a differential seasonal variation of K values between the various year-groups which is quite suggestive. The males and females of the length-group 12–16 cm. show a bigger seasonal variation than the others. Hart (1946) also observed a similar differential variation in *Merluccius hubbsi*. He explained the anomaly as due to inadequate sampling. Selective sampling may have contributed to the differential variation in *Gadus minutus* also to some extent, but the length-group 12–16 cm. consists of I, II and III groups of males and I and II groups of females, and are mostly spawners for the first and second time. It is probable that the earliest spawnings in the life history of such a short-lived fish are the most important in contributing to a potential increase and stabilization of the population (i.e. contribute a relatively larger bulk of reproductive products), and this may be one of the major causes for the differential variation of K values between particular length-groups.

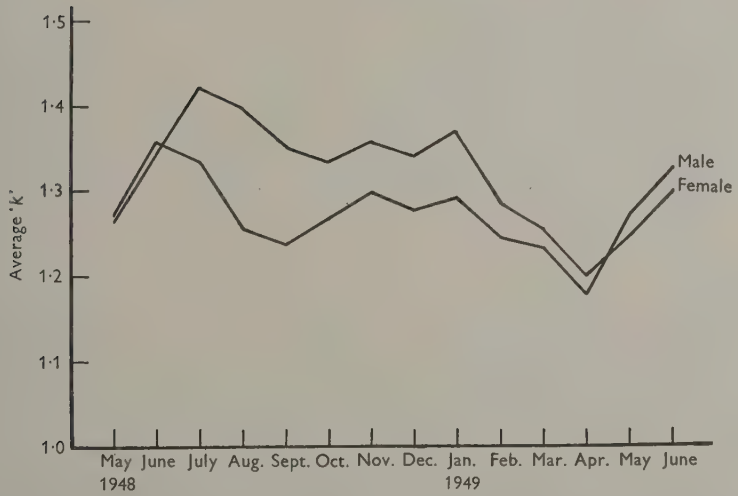
There is no evidence from ponderal index variation or direct observation to suggest that the older age-groups spawn earlier than the younger. The spawning periods in all the groups synchronize. There is no shoreward movement of the older and larger groups occurring earlier than the smaller ones similar to the movements observed by Hickling (1930) in *Merluccius merluccius* and Hart (1946) in *M. hubbsi*. Unlike the long-lived hake, the poor-cod is not an off-shore fish and its total span of life is small. Its distribution is limited within the 200 m. contour, and the population here studied was sampled only

within some 15 miles of the coast, so that any possible migration towards shallower regions is scarcely apparent.

The males in general show a lower K value throughout the spawning and growing periods than do the females. This agrees with Hickling's (1930)

TABLE XXV. PONDERAL INDEX K FOR THE WHOLE SAMPLE IN EACH MONTH

Month	Female	Male
May 1948	1·263	1·265
June	1·347	1·356
July	1·422	1·347
Aug.	1·398	1·254
Sept.	1·351	1·237
Oct.	1·334	1·266
Nov.	1·350	1·296
Dec.	1·327	1·277
Jan. 1949	1·369	1·290
Feb.	1·283	1·234
Mar.	1·254	1·232
Apr.	1·158	1·179
May	1·248	1·283
June	1·300	1·330



Text-fig. 16. The mean K values for the whole sample of fish in successive months.

observation that the metabolic strain of spawning is greater in males than in females; but the recovery from the metabolic stress appears to be more rapid in the male than in the female when spawning is over.

The average ponderal index has also been calculated for the whole sample of fish of either sex in each month to examine whether by treating the data from bulk sample there is any marked departure from the observations on individual length groups. These monthly averages are given in Table XXV.

These values have been plotted as two curves in Text-fig 16, which indicates

the same trend of events as deduced from the variations in condition of individual length-groups. The spawning period is clearly defined as between February and May and the recovery of males after spawning is more rapid than that of the females.

That the main spawning period of *Gadus minutus* is from February to May is further shown by analysis of the data on the seasonal occurrence of the post-larvae in the Plymouth region. The data are given in the records of Russell (1930–47) and Corbin (1948) from their routine sampling of the young of teleostean fishes in the Plymouth area, covering the periods 1924–39, and 1946 onwards. These data have been abstracted in Table XXVI.

TABLE XXVI. AVERAGE MONTHLY CATCHES OF POST-LARVAE OF *GADUS MINUTUS* PER HALF-HOUR OBLIQUE HAUL WITH THE 2 M. RING TRAWL

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
1924					33·9	24·9	4·2					
1925				42·9	49·8	4·8	..	..				
1926				56·1	40·2	12·9	..	..	..			
1927				17·4	43·2	..	..	..	..	..	..	..
1928	..	3·9	24·0	135·6								
1929				10·5	0·9	1·2	0·3	..	..	..		
1930		..	..	19·0	37·0	+	..	..	..	..	..	..
1931	..	9·0	175·0	80·0	18·0	..	..	..	..	..	..	..
1932	..	..	1·0	10·0	52·0	1·0	..	..	..	..	..	..
1933	..	..	21·0	12·0	1·0	..	..	..	..	..	..	..
1934	..	..	2·0	17·0	19·0	..	..	..	..	..	..	..
1935	..	..	1·0	1·0	5·0	..	..	..	..	..	..	..
1936	..	+	1·0	1·0	1·0	4·0	..	..	..	..	..	..
1937	..	..	10·0	2·0	1·0	1·0	+	..	..	..	..	..
1938	..	7·0	..	5·0	+	..	..	..	..	..	..	..
1939	..	..	..	..	+	..	..	..	..	..	..	..
1946						..	2·0	..	..	..	..	..
1947	..	..	2·0	1·0	2·0	..	..	..	..	..	..	..
Av.	..	1·7	19·8	25·7	19·1	2·9	0·4	..	..	..	..	..

The mean numbers of post-larvae of *G. minutus* (per ½ hr. oblique haul) for each month have been totalled, and averages derived for each month. The result shows clearly that the post-larvae of *G. minutus* occurred only in the hauls of February, March, April, May, June and July. The numbers in February and June were very small and still smaller in July. From the analysis of the ponderal indices it was inferred that the spawning period is from February to May, the height of spawning being in March and April. The number of post-larvae is greatest in April and May. The occurrence of a few post-larvae in June and July may be due to a few late spawners as well as to a few post-larvae being carried over to these months, for there are no data regarding the size of the post-larvae recorded. Thus the post-larvae recorded in the months of June and July may include the slower-growing individuals from earlier spawnings.

When the individual years are considered there is a certain amount of fluctuation in the general picture, the post-larvae occurring earlier in some years

and later in others. The maximum number of post-larvae occurred in March or April in some years and in May in others. Table XXVII gives the number of times the post-larvae have occurred in the hauls (*not* numbers of larvae) in individual months during the period under survey.

It is seen from Table XXVI that there has been a gradual decline in the occurrence of post-larvae of *G. minutus* in Plymouth waters in recent

TABLE XXVII. OCCURRENCES OF POST-LARVAE IN PARTICULAR MONTHS

Month	No. of Occurrence	No. of years covered
Jan.	0	11
Feb.	4	12
Mar.	9	12
Apr.	15	16
May	16	16
June	8	17
July	4	17
Aug.–Dec.	0	13–16

years. In the collections from the Young Fish Trawl for 1948–49 only three post-larvae have been found of *G. minutus* in forty-eight hauls and of these, two post-larvae occurred in April 1949 and one in June 1948. This decline in the occurrence of post-larvae of *G. minutus* may be only a part of the general decline of post-larvae of all teleostean fishes in Plymouth waters observed by Russell. This decline is thought to be due to a decrease in the amount of rich Atlantic surface water entering the western channel, so that the more localized stocks of fish have spawned under adverse conditions, resulting from an increased proportion of comparatively impoverished coastal water.

SUMMARY

The volumetric and qualitative analysis of the food of *Gadus minutus* has been discussed. The post-larvae feed entirely on copepods, mostly *Pseudocalanus elongatus*. The O-group feeds on copepods, small decapods, amphipods, polychaetes and isopods. The adolescent and adult groups feed on larger decapods like *Processa canaliculata*, *Galathea* spp. and *Portunus* spp., fish, polychaetes and amphipods.

The age and rate of growth of *G. minutus* have been computed from a study of the supra-occipital crest. These age determinations have been correlated with the age determined by scales, otoliths and size-analysis. Back-calculations have been made by graphical method and by using the Lea-Dahl formula. The differences between the back-calculated lengths and actual observed lengths are negligible.

The spawning period has been determined by analysis of the seasonal fluctuation of the condition factor of the fish. This has been verified by examination of the data on the seasonal abundance of the post-larvae in the Plymouth area. The spawning period is from February to May and the height of spawning is in March and April.

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[1] I am grateful to Mr Michael Graham for sending me this paper.

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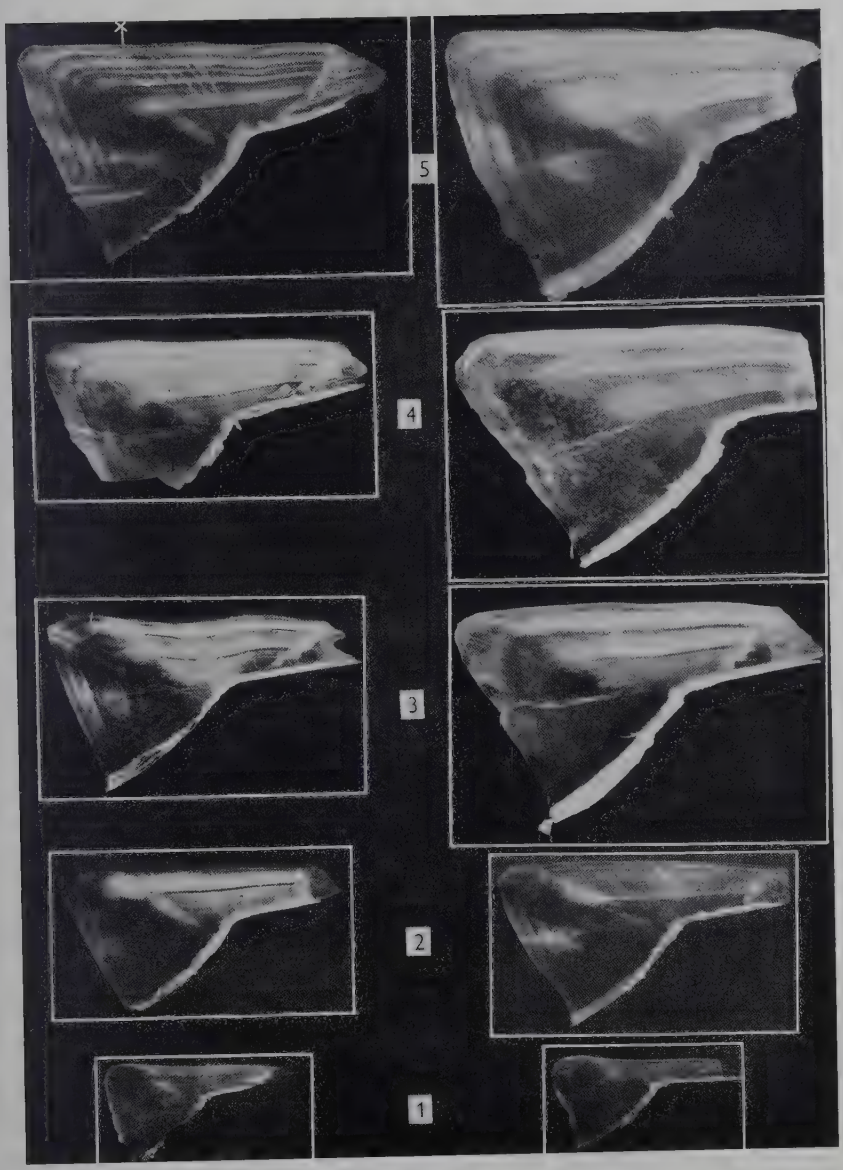
Appendix. List of Organisms Found in the Stomach Contents of *Gadus minutus*

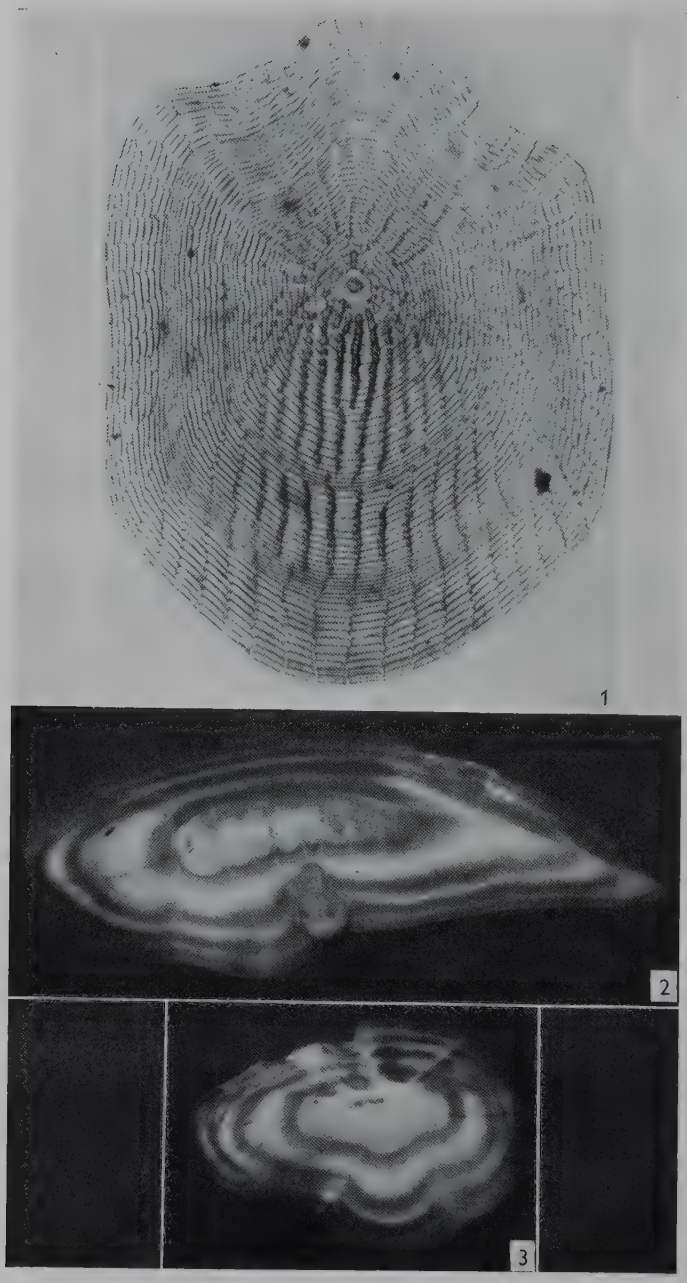
Food of I- to V-Year Groups of Gadus minutus

Polychaeta	*Goniada* sp.
	Pallasia murata
	Amphitrite sp.
Crustacea	
Copepoda	*Calanus finmarchicus*
	Labidocera wollastoni
Cumacea	*Diastylis* sp.
Leptostraca	*Nebalia bipes*[1]
Isopoda	*Rocinela danmoniensis*
	Conilera cylindracea
Amphipoda	*Orchomenella nana*
	Ampelisca brevicornis
	A. spinipes
	A. tenuicornis
	A. diadema
	Leucothoë sp.
	Panoploea minuta
	Iphimedia obesa
	Urothoë elegans
	Monoculodes carinatus
	Monoculodes sp.
	Apherusa ovalipes
	Apherusa henneguyi
	Nototropis falcatus
	Cheirocratus assimilis
	Maera othonis
	Erichthonius brasiliensis
	Eurystheus maculatus
	Phtisica marina
	Pseudoprotella phasma
Mysidacea	*Leptomysis gracilis*
	Anchialina agilis
Euphausiacea	*Nyctiphanes couchi*
Decapoda	*Pandalina brevirostris*
	Hippolyte varians
	Spirontocaris cranchi[1]
	Processa canaliculata
	Crangon vulgaris
	Philocheras bispinosus
	Galathea intermedia
	G. dispersa
	G. strigosa[2]
	Munida bamffica[1]
	Porcellana longicornis
	P. platycheles
	Upogebia sp.
	Eupagurus bernhardus
	E. prideauxi
	Portunus pusillus
	P. holsatus
	P. depurator
	Corystes cassivelaunus[3]
	Inachus dorsettensis
	Macropodia longirostris
Mollusca	*Nucula nitida*
	Natica catena
	Turritella communis
	Philine aperta[4]
	Heterosepiola atlantica[3]
Echinodermata	*Ophiura texturata*
	Cucumaria sp.[3]
Fish	*Gadus minutus*?[1]
	Callionymus spp.
	Crystallogobius nilssoni
	Trigla spp.
	Ctenolabrus sp.

[1] Occurred only twice.
[2] Occurred only in twelve stomachs.
[3] Occurred only once.
[4] Occurred only thrice.



A B



Figs. 1–3.

Food of the O-Group of Gadus minutus

Polychaetes	*Goniada* sp.	Decapoda	*Pandalina brevirostris*
Crustacea			*Hippolyte varians*
Copepoda	*Calanus finmarchicus*		Small *Processa canaliculata*
	Pseudocalanus elongatus		
	Centropages typicus		*Crangon vulgaris*
	Temora longicornis		*Philocheras bispinosus*
	Acartia clausi		*Galathea intermedia*
Isopoda	*Conilera cylindracea*		Small *Porcellana longicornis*
Amphipoda	Small *Ampelisca spinipes* and *A. diadema*		*Eupagurus bernhardus*
	Apherusa ovalipes		Small *Portunus* spp.
	A. henneguyi	Mollusca	*Nucula nitida*
	Phtisica marina		*Natica catena*
Mysidacea	*Leptomysis gracilis*		Small *Turritella communis*
Euphausiacea	*Nyctiphanes couchi*		

EXPLANATION OF PLATES

Plate I

Ten supra-occipital crests of *Gadus minutus* photographed against a black background by reflected light. ×3·8.

A, five supra-occipital crests belonging to male *Gadus minutus* measuring (1) 8·0 cm.—age 1; (2) 12·4 cm.—age 2, just completing the 2nd transparent zone; (3) 14·6 cm.—age 3; (4) 16·5 cm.—age 4, just completing the 4th transparent zone; (5) 18·1 cm.—age 5 (the ring marked *X* is a false one caused by 'doubling': it can be seen that this ring is not complete and becomes continuous with the succeeding transparent zone in the vertical portion of the crest). B, five supra-occipital crests belonging to female *Gadus minutus* measuring (1) 8·4 cm.—age 1; (2) 13·4 cm.—age 2; (3) 16·4 cm.—age 3; (4) 18·8 cm.—age 4; (5) 21·1 cm.—age 5.

Plate II

Fig. 1. A scale from a male *Gadus minutus* measuring 14·9 cm. The photograph is of an alizarine-stained scale. ×42.

Fig. 2. Longitudinal section of the otolith of a female *Gadus minutus* measuring 18·8 cm. Four opaque zones and four transparent zones are clearly visible. The 4th transparent zone is at the margin. This is one of the very few of the older fishes in which the 'age rings' could be so clearly discerned in the otolith. ×11·5.

Fig, 3. The transverse section of the above same otolith. ×11·5.

ADVANCES IN THE PHYSIOLOGY OF PERIPHERAL NERVE

By D. K. Hill

Lately physiologist at the Plymouth Laboratory

The last 20 years have seen many advances in our knowledge of the mechanisms responsible for the transmission of impulses in peripheral nerve fibres. This has come about largely through researches on the nerves of marine invertebrates. Much of the work has been done at Plymouth. The purpose of this article is to give some of the reasons why certain features of these nerves, which distinguish them from the nerves of vertebrates, should make them so desirable for experimental work.

The giant nerve fibre of the squid did not come into the limelight until the middle nineteen-thirties, nor did the other smaller single fibres which can be dissected out of the nerve trunks of cuttlefish, crabs and lobsters. Before describing the work with single fibres, we will go further back to about 1926 when, as the result of work by A. Levin at Plymouth, it was realized that the multi-fibred limb nerves of Crustacea were highly suitable for studies of the effect of activity on nerve metabolism.

Multi-fibred Invertebrate Nerves

For many years it had been believed that in the transmission of nerve impulses no heat is evolved. Until the end of the last century practically all views attributed to nerve a completely passive role in the conduction of an impulse. As recently as 25 years ago the impulse was pictured, in Sir William Bayliss's words, as a 'reversible physico-chemical process, not associated with loss of material on account of metabolic reactions'. However, this was wrong. Heat is set free, but its amount was too small to detect. A. V. Hill finally demonstrated this phenomenon in frog's nerve: but, as he said (in 1932): 'physiological laboratories ought to be built near the sea, or at least within reach of aquaria where delicate marine animals could be stored. The heat production of crab's nerve could have been measured 20 years ago: actually 14 years were wasted before it was measured in frog's nerve.' Whereas, by 1930, it had become possible to measure the heat production following a single impulse in the crab's nerve, in frog's nerve, where much less is produced, 100 impulses are required.

Heat production is only one sign of metabolism. In every aspect the extra metabolism due to stimulation of a crustacean nerve is much greater than it is in the frog's nerve. This superior efficiency of the frog's nerve is evident in

its comparative resistance to fatigue: it can continue to pass impulses at a high frequency for a long time, while the crab's nerve fatigues rapidly. We now understand the reason for this difference. The fibre of a vertebrate nerve possesses a myelin sheath, composed of lipoid material, which in effect 'insulates' the fibre except at the nodes of Ranvier, where the sheath is absent. It has recently been shown that the nervous impulse progresses by 'jumping' from node to node. This means that the active process, which spreads over the whole membrane in the invertebrate non-myelinated fibre, affects only that part of the frog fibre which is free from the myelin covering, so it is only in the region of the nodes that any extra metabolism occurs when the fibre becomes active. The whole of the inter-nodal part of the fibre is a purely passive bridge with quite simple electrical properties, doing no more than enable one node to excite the next. The frog fibre is only 10 μ across, but the nodes may be 2 mm. apart, so the area of membrane involved in activity is very small. Apart from the greater economy which goes with this ingenious mechanism, there is the added advantage that considerably faster transmission is possible with a given size of fibre.

The two features of invertebrate nerve which the physiologist finds so much to his advantage, namely the high rate of metabolism and the occasional appearance of large fibres, might neither have been found if the myelin sheath had been developed in this type of nerve. One can think of only two possible reasons why the large fibre evolved: first, because a large fibre conducts faster than a small one, and at a higher frequency; secondly, because a large fibre is more resistant to fatigue than a small one, for the surface activity is supported by a relatively larger volume of axoplasm (the name given to the interior substance of a nerve fibre). One advantage of fast transmission is plain enough, reaction times are reduced; but there is another, more subtle, reason which may be suggested. A large muscle mass as, for instance, the mantle muscle of the jet-propelled squid, may have to be synchronously activated in all its parts from one ganglion. Low-velocity fibres would produce a *wave* of contraction, inefficient for propulsion, while high-velocity fibres can be sufficiently graded in size (the larger, faster fibres going to the more distant part of the muscle) to provide a synchronous burst of impulses at all nerve endings in the muscle.

Turning to the question of resistance to fatigue, we now know enough about the actual quantities of ions traversing the active membrane to be able to calculate the extent to which a nerve fibre is 'run down' when an impulse passes along it. The fibre loses some of its internal potassium and gains sodium from the outside when it is stimulated, and it takes many minutes for the original balance to be restored. The nerve can pass 100 impulses per sec. (the giant fibres up to 500 per sec.), but the axoplasm of the smallest fibres does not constitute a sufficient reserve for prolonged activity at high frequency; even after 10–20 sec. perhaps as much as a half of the internal potassium would

be lost from a 1 μ fibre. However, the very small fibres probably have a sensory function, or at any rate a function which normally requires them to pass but few impulses in a minute, so the axoplasm may well provide an adequate reserve. On the other hand, the muscles of the leg require innervation by nerve fibres which are less prone to fatigue, for they must be capable of passing impulses at high frequency, and bursts of activity may be required in quick succession.

It is not possible to be sure which of these factors has been predominant in the evolution of the larger motor fibres. Both the resistance to fatigue and the higher velocity of transmission could have been achieved by the myelin sheath, but luckily for the physiologist, another and more clumsy solution was found for the invertebrate!

Within the last 15 years advances have been made in our knowledge of the ionic equilibrium which determines the electrical potential across the membrane, and in connexion with the passage of ions across this membrane when the nerve is stimulated. It has been possible, for instance, to measure the amount of potassium which escapes from the fibres of a crustacean nerve when it is stimulated. It is improbable that this could have been done with a frog's nerve, for the ionic currents, being presumably confined to the small areas of membrane around the nodes of Ranvier, would be too small to measure.

There is another sign of activity, easily measured in a non-myelinated nerve trunk, which is so small as to be quite undetectable in a frog's nerve: this is the change in the intensity of light scattered by the nerve when it is stimulated; it is thought to be caused by a minute swelling of the individual nerve fibres.

Isolated Nerve Fibres

Research with single fibres started about 1935, following J. Z. Young's histological studies of the nerves of Crustacea and Cephalopods. Before describing some of the things which can be done with the giant fibre of the squid, reference will be made to the work with isolated crustacean nerve fibres. The great majority of the fibres of a crustacean nerve trunk, tens of thousands of them, are very small, having diameters between 0·5 and 5 μ; the function of these fibres is not certain, but they are probably mostly connected with sensory endings. In addition to the very small fibres there are larger ones supplying the muscles. These motor fibres are relatively very few, being numbered in tens rather than in thousands, and the largest are 25–80 μ in diameter. By skilful dissection these large fibres can be isolated singly, they can be manipulated without much difficulty, and will survive and respond to stimulation for many hours in artificial saline solution. A fibre of this sort is not large enough for insertion of a micro-electrode, nor is it suitable for the other purposes which make the squid fibre so useful, such as the chemical analysis of the constituents of the axoplasm. In other words, the single

crustacean fibres can only be operated on by techniques generally used for multi-fibred bundles of nerves. What, then, is gained by using the single fibre? Why would not bundles of smaller fibres—much more easily prepared—serve just as well? Briefly, the answer can be given as follows. The physiology of peripheral nerves has reached a stage where really accurate quantitative facts and figures are required. These cannot be obtained from the multi-fibred preparation, as some examples will show. (i) Inorganic ions cross the membrane of a nerve fibre when it is stimulated: we want to know, accurately, the quantities of ions which pass a unit area of membrane per impulse. These can be measured by radio-active tracers and other methods. The difficulties of doing this accurately with a bundle of fibres are obvious enough. The fibres are of different sizes, one cannot be certain that they are all excitable, and complicated (and approximate) corrections have to be made for diffusion between the inter-fibre spaces and the exterior bulk of the solution. (ii) The electrical resistance and capacity of the nerve membrane must be measured. This can be done accurately only with a single fibre, where all the quantities involved can be determined precisely. (iii) We wish to be able to make a rapid change in the composition of the fluid surrounding the fibre. With fibres in a bundle this is not possible, for diffusion is too slow; the ions or other chemical substances would not enter or leave the inter-fibre spaces sufficiently rapidly. (iv) For certain purposes it is necessary to work with a fibre which is surrounded by only a very small volume of electrolyte solution: to do this the fibre is transferred into paraffin oil. Under such conditions it still conducts, even though the external solution occupies a layer only a few microns thick.

The Giant Fibre

The mantle muscles of the squid and cuttlefish are supplied by nerve fibres which radiate out from the stellate ganglia. These are the so-called giant fibres. The largest are found in the squid: they may be 500–800 μ in diameter. By virtue of their large size they allow certain procedures which are not applicable to smaller fibres. An isolated fibre can be cannulated at its cut end, and a thin rod-like electrode (or even a double electrode, consisting of two independent wires wound helically around a fine glass rod) can be inserted through the cannula, and pushed down so far into the interior of the fibre that the active part of the electrode may be some centimetres from the cut end. Surprisingly enough, this operation does not destroy the excitability of the fibre, and it may conduct impulses, and to all intents and purposes be in perfect condition, for many hours after the electrode has been inserted.

The reason for wanting an internal electrode can be explained as follows. In the unstimulated fibre there is a potential difference across the membrane amounting to about 50 mV. This is known as the 'resting potential' and is in the sense of the interior of the fibre being negative with respect to the outside.

In a multi-fibred nerve trunk, or in a small fibre, the resting potential cannot be measured accurately, because it is difficult to make electrical connexion with the axoplasm in the intact part of the fibre which is conducting the impulse. The best that can be done is to make connexion with the axoplasm at the ends of the fibre: this is achieved by some form of chemical or mechanical injury to the ends, which has the effect of breaking down the electrical resistance of the membrane, thus allowing more or less direct connexion with the inside. But, owing to short circuits, one can only tap off a rather unknown fraction of the true membrane potential in this way. The insertion of an electrode into the inside of a giant fibre is a means of overcoming the difficulty; one can then record the full potential, either at rest or during the passage of an impulse. Leading off from the *outside* of the fibre is easily achieved; all that is needed is an electrode in the conducting electrolyte solution in which the active part of the fibre is bathed. An amplifier and cathode-ray tube are used for recording the membrane potential.

The earliest experiments with the internal electrode led to a rather surprising discovery. It had always been tacitly assumed that activity simply involved a transitory disappearance of the resting potential. Recordings made with external electrodes were not sufficiently reliable for this assumption to be seriously challenged. Experiments with the internal electrode showed that the membrane potential actually *reverses* its sign as the impulse passes. Further experiments have suggested that the reversal is caused by a large increase in the permeability of the membrane to sodium ions. The concentration of sodium ions in the axoplasm is very low, so there is a gradient tending to drive them in from the outside, and the negatively charged interior of the resting fibre also tends to draw in the positively charged sodium ions. A sudden breakdown in the barrier will allow sodium ions to rush in, the membrane potential will fall as the negative charge inside is satisfied by the positive sodium ions, and if the permeability becomes high enough, and the increase is preferentially in favour of sodium, the potential will actually reverse—but one gets into rather deep water here in attempting to explain it. At all events, there is now good support for the view that the action potential is primarily due to a sudden inrush of sodium. To elucidate this matter further, A. L. Hodgkin, A. F. Huxley and B. Katz have used a double internal electrode, one wire of which forces the membrane potential to change in a prescribed manner—it constrains the membrane, as it were, to pass through an abnormal action potential cycle—and the other wire records the current which flows across the membrane as the result of this. The problem, both from the technical and theoretical aspects, has become rather complicated; the findings have not yet been published.

Another facility is afforded by the large size of the squid fibre. The volume of the axoplasm is sufficient to allow analysis of its constituents. The quantities of the various inorganic ions can be estimated, the identities and amounts of the internal amino-acids, which play a part in maintaining the ionic balance,

can also be determined. The axoplasm is squeezed out of the fibre for such analyses. It is found to be of a jelly-like consistency, and other than straight chemical tests can be made: for instance, it is found that the addition of a small quantity of calcium to the solution into which the axoplasm is extruded will cause rapid solution of the jelly. Electron microscopy of the axoplasm has revealed elongated filaments showing fine striations.

A major problem which has to be faced by anyone who embarks on research with the giant squid fibre is that of obtaining living squid. With all the resources of the laboratory at Plymouth, and although squid are plentiful in the sea at most seasons of the year, the conditions are such that a specimen which is capable of living for more than 12 hr. in the laboratory tanks is a rarity. The cuttlefish is a hardier animal and will live for a long period in captivity. Unfortunately, its nerve fibres are not so large as those of the squid, being only about 150μ in diameter, and no one has attempted to insert an internal electrode through the cut end of such a fibre. However, they are large enough to possess one advantage over the crustacean fibres because the volume of a single fibre, perhaps 4 cm. long, is just great enough to allow quantitative analysis of its constituents, and an attempt has recently been made to measure the amount of sodium which enters the fibre as the result of activity. Radioactive tracers can be used to follow movements of ions through the membrane, both at rest and when it is stimulated: it is true that this is possible also with the smaller crustacean fibres, but the improvement in accuracy which goes with the use of a larger fibre makes the cuttlefish especially valuable for such purposes.

Conclusion

It should be clear why the nerves of marine animals are much sought after. There is no reason to suppose that, in essential details, the changes in the membrane of the non-myelinated fibre which occur in activity do not also take place at the nodes of Ranvier in a myelinated nerve. The saltatory progression of the impulse in the myelinated nerve is due to a mechanism which should probably be considered as an added, and not very mysterious, refinement. The electrical excitation of one node by another is thought to involve essentially the same process as is found in non-myelinated nerve, by which one part of the membrane is excited by an adjacent one. The vital 'explosive' change at the membrane forms the subject of the most intriguing current research on peripheral nerve, and as it may be predicted that this change, if it is ultimately sufficiently understood, will be found to be fundamentally the same in both types of nerve, one may conclude that much has been learned about vertebrate nerves by studying those of invertebrates.

NOTES ON THE PLYMOUTH MARINE FAUNA

AMPHIPODA

By G. M. Spooner

The marine Amphipoda of the Plymouth area, as a group, were last given attention in the middle 1930's by Crawford (1936, 1937). Renewed investigation after the lapse of 15 years has indicated that knowledge of species present was by no means complete, or that some changes have occurred in the interval, or both. In a recent survey of the amphipod fauna of the Isle of Man, Jones (1948) found no indication of the existence of undescribed species, nor even of known species previously unrecorded from Britain. The experience at Plymouth has been quite the reverse.

I am grateful to Mr M. D. Menon and to Dr H. W. Chang for giving me the chance of examining amphipods from the stomachs of *Gadus minutus* L.* and *Callionymus lyra* L. respectively. The use of bottom-living fish as a method of collecting amphipods has much to commend it, as records will testify.

The genera *Gammarus*, *Marinogammarus*, and *Corophium* are not included, being reserved for separate treatment. An asterisk indicates that the species have not hitherto appeared in a list of the Plymouth marine fauna (Marine Biol. Assoc., 1931, supplemented by Crawford, 1936).

Additions to the fauna show a notable balance of species which occur to the southward or in warmer waters. Taken together the evidence provided for a certain northward spread of the fauna cannot be ignored.

Family **Lysianassidae**

PERRIERELLA AUDOUINIANA (Bate)

Plymouth; dredgings from Asia Shoal, 2. vi. 49, ♀♀.

LYSIANASSA CERATINA (A. Walker)

Wembury Point, L.W. sievings.

*SOCARNOPSIS CRENULATA Chevreux [Chevreux, 1910, pp. 165–9, fig. 2; Chevreux & Fage, 1925, pp. 48–50, figs. 31, 32]

One ♀ amongst small sample of bottom fauna of L4, 3. vi. 49; length 9 mm., as against maximum of 7 mm. given by Chevreux & Fage. Genus and species new for Britain: previous northerly limit was Brittany.

TRYPHOSA SARSI Bonnier

Salcombe; Castle Rocks, L.W. sievings, 12. v. 49, ♀♀.

* See Menon, 1950: this *Journal* pp. 186–198.

ORCHOMENE HUMILIS (A. Costa) (=*batei* Sars)
Salcombe; Castle Rocks, L.W. sievings, 12. v. 49, ♀.

ORCHOMENELLA NANA (Kröyer)
Wembury Point, L.W. sievings. Stomachs of *Gadus minutus*, June 1948, ♂♀♀.

Family **Ampeliscidae**

AMPELISCA SPINIPES Boeck
Regularly in stomachs of *Gadus minutus* from the trawling grounds, including large specimens up to 18 mm. long. Present at station L4 and in the Mewstone shell gravel.

AMPELISCA DIADEMA (A. Costa)
Frequent in stomachs of *Gadus minutus*, 1948.

AMPELISCA TENUICORNIS Lillj.
A few in stomachs of *Gadus minutus* 1948, more freely in *Callionymus lyra* 1949.

AMPELISCA BREVICORNIS (A. Costa) (=*laevigata* Sars)
Two adults from stomachs of *Gadus minutus*, 1948.

*AMPELISCA sp. (allied to *brevicornis*)
Stomachs of *Gadus minutus*, 2♂♂, 1 juv., June 1948.
An apparently undescribed species, most closely related to *A. brevicornis*, which it resembles in the form of pp. 7, in the form of pp. 3, and in the shape of the head. It differs notably in the more feeble invagination at the posterior corner of epimeron 3, in the presence of a raised hump dorsally on the anterior half of urosome segment 1, in the ciliation of uropod 3, and small differences in antenna 1.

Family **Haustoriidae**

HAUSTORIUS ARENARIUS (Slabber)
Salcombe; Mill Bay, several in the sand in the lower part of the tidal zone, 17. iii. 49. Formerly not found in the Salcombe Estuary, and its presence at Mill Bay doubtless the result of the accumulation here of sand described by Wilson (1949). Otherwise recorded only from Whitsand Bay.

UROTHOË ELEGANS Bate
One in stomach of *Gadus minutus*.

Family **Phoxocephalidae**

HARPINIA ANTENNARIA Meinert
Rame Mud, 12. vii. 39 (M. Mare), three from a grab haul.

Family **Amphilochidae**

AMPHILOCHUS NEAPOLITANUS Della Valle
Salcombe, Castle Rocks, 12. v. 49, 3♀♀ breeding.

Family **Leucothoidae**

LEUCOTHOË SPINICARPA (Abildg.)

From cavities in the sponge *Desmacidon*, Mewstone grounds; from amongst hydroids and sponges from Plymouth Sound; etc. One in a stomach of *Gadus minutus*.

*LEUCOTHOË sp. (allied to *L. richiardi* Lessona)

From stomachs of *Gadus minutus*, two in June 1948, one in Nov. 1948. Two of the specimens are undamaged. This species differs from *L. spinicarpa* in its posteriorly incised epimeron 3, and in its weaker gnathopod 1 dactyl which is only one third the length of the propod. It is possibly identical with the Mediterranean species *L. richiardi*, of which Della Valle (1893) gives a description and figures. Alternatively, it may be the undescribed species discovered by Crawford in *Chaetopterus* tubes (Crawford, 1936, p. 102).

LEUCOTHOË LILLJEBORGI Boeck

Rame Mud; 12. vii. 39 (M. Mare), four specimens in grab sample.

Family **Stenothoidae**

STENOTHOË MONOCULOIDES (Mont.)

From sievings of stones and rocks near L.W. below the Laboratory, at Rum Bay, Wembury Point and at Salcombe Castle Rocks, ♀♀.

*STENOTHOË sp. (allied to *monoculoides* and *spinimana*)

A number of ♀♀, many breeding, from among hydroids collected in Mill Bay Docks, 7. vi. 49. Others from hydroids on raft near Breakwater, end March 1950.

This is apparently a distinct species, somewhat intermediate between *S. monoculoides* and the south-european *S. spinimana* Chevreux (Chevreux & Fage, 1925, pp. 134–5, fig. 133), but reaching a slightly larger size than either. The gnathopods I and II agree with those described for *S. spinimana*, and so provide a good distinction from *S. monoculoides*. There are four spines laterally on uropod 3 peduncle, and the number of antennal segments is intermediate between the two species mentioned. The telson, however, is unarmed, and in certain other respects the resemblance is to *monoculoides* rather than to *spinimana*.

The colour pattern was noted as follows: body translucent, especially the urosome; middle of body with broken dark lines between the segments round which orange patches develop; other irregular orange patches on side plates; eye carmine.

*STENOTHOË VALIDA Dana [Chevreux & Fage, 1925, pp. 137–8, fig. 137]

♂ and ♀ (with eggs) from hydroids collected in Mill Bay Docks, 7. vi. 49, in company with the foregoing. Further ♂♂♀♀ from hydroids on raft near

Breakwater, end March 1950. A large species for a *Stenothoë*, with distinctive characters. Wide-spread in warm waters and known from the south of France. The colour pattern was noted as follows: body translucent, with scattered reddish orange and orange marks; a large red-orange mark on the urosome providing a striking feature.

Family **Phliasidae**

PEREIONOTUS TESTUDO (Mont.)

Wembury Point, from sievings of stones and weeds near L.W., 12. iv. 49, five specimens. Again 18. iii. 50, four specimens from pools above L.W.N. In the laboratory they were observed to browse on living fucoid fronds, scraping small patches off the surface. A curious species, seldom encountered: formerly taken at Salcombe by Norman.

Family **Acanthonozomidae**

PANOPLOEA MINUTA (G. O. Sars)

Two in stomachs of *Gadus minutus*, 1948.

PANOPLOEA EBLANAE (Bate)

Rame grounds, ♀ from side of trawl, 8. iv. 49.

IPHIMEDIA OBESA Rathke

A few in stomachs of *Gadus minutus*, 1948.

Family **Oedicerosidae**

*MONOCULODES sp. (? TESSALATUS Schneider)

From stomach of *Gadus minutus*, July 1948, one. Differs from other European species, except *M. tessalatus*, in the proportions of the gnathopod segments. If indeed this be *tessalatus*, which is a northern species, it has not previously been found so far south.

Family **Calliopiidae**

APHERUSA BISPINOSA (Bate)

Salcombe, Castle Rocks, L.W. sievings, 12. v. 49, abundant, ♀♀ greatly in excess of ♂♂.

APHERUSA OVALIPES Norman & Scott

One of the principal species in stomachs of *Gadus minutus*, particularly in June and July.

*APHERUSA HENNEGUYI Chev. & Fage [Chevreux & Fage, 1925, pp. 180–1, figs. 185, 186]

Regularly in the stomachs of *Gadus minutus*, 1948, though less numerous than the above (about sixty-five specimens seen). Present also in a small sample of the ground fauna at station L4 on 3. vi. 49.

Known originally to Chevreux & Fage from only one locality (160 m., S.W. of Belle-Isle), this species has not previously been recognised in British waters. In view of Crawford's investigation (1937) on bottom-living amphipods, it is difficult to escape the conclusion that the species has spread into the Plymouth area but recently.

APHERUSA CIRRUS (Bate) (=*borealis* Sars)

A few in L.W. sievings among rocks at Wembury Point and Salcombe Castle. A uniform rose-pink colour seems distinctive.

*CALLIOPIUS LAEVIUSCULUS (Kröyer)

Salcombe, Castle Rocks, L.W. sievings, 12. v. 49, one. Known from localities in Cornwall, N. Devon, and occurrence in the Plymouth area to be anticipated (Crawford, 1936, p. 101).

The characters agree with Sars's figures of *C. rathkei*, which is assumed to be synonymous (following Stephensen).

Family **Melphidippidae**

MELPHIDIPPELLA MACRA (Norman)

From stomach of *Gadus minutus*, 3. vi. 49, ♀.

Family **Gammaridae**

*CHEIROCRATUS ASSIMILIS Lillj. [Chevreux & Fage, 1925, p. 225, fig. 235]

One ♂ from stomach of *Gadus minutus*, July 1948.

PHERUSA FUCICOLA Leach

Freely under stones, etc., near L.W., Plymouth (Rum Bay), Wembury Point, and Salcombe. Salstone, one ♂.

*MELITA HERGENSIS Reid

A characteristic species on the shore under stones, etc., in L.W. region, where it replaces *M. palmata* (Montagu). At once recognized in the field by its blue-grey colouring, broken only by white bands on the limbs which show up on closer inspection.

First taken at the mouth of the Yealm, near L.W., 3. viii. 38, when recognized as a distinct species. Independently Reid (1939) described the species, having taken it from Wembury Bay.

Amongst specimens from various parts of the coast identified by Reid in the British Museum were some from Salcombe and Polperro (Norman collection).

It has since been found freely at Rum Bay, Mt. Edgcumbe, Wembury Point, and Salcombe Castle Rocks.

Some former records of *M. palmata*, especially from the sub-littoral zones, may be expected to belong to *M. hergensis*.

MELITA GLADIOSA Bate

Salcombe, Castle Rocks, 12. v. 49, adult ♂.

MELITA PELLUCIDA G. O. Sars

Tamar Estuary, in reed bed near Cotehele, 10. iii. 48, about forty. Also obtained in the Helford River, W. Cornwall, at the head of Frenchman's Creek, Sept. 1949.

Family **Dexaminidae**

DEXAMINE THEA Boeck

Salcombe estuary, at Castle Rocks and the Salstone, May 1949, ♀♀ and juv., accompanying *D. spinosa* (Mont.), amongst weeds.

Family **Aoridae**

AORA TYPICA Kröyer

Salstone, 13. v. 49, both sexes freely, sieved from weeds near L.W.

MICRODEUTOPUS CHELIFER (Bate)

Wembury Point, 12. iv. 49, sieved from weeds, breeding.
Salcombe, Castle Rocks, 12. v. 49, ♀.

MICRODEUTOPUS DAMNONIENSIS (Bate) [=*propinquus* Sars]

Salstone, sieved from weeds at L.W., ♂♂♀♀.

From examining ♂♂ of different sizes it is clear that the species recognized by Chevreux & Fage (1925) as Bate's *damnoniensis* is identical with the species figured and described by Sars (originally as *propinquus*). Chevreux & Fage, however, cannot have seen fully mature specimens in which the secondary tooth on the carpus of gnathopod 1 had developed. The gnathopod 1 figured by them (fig. 308) is correct for younger ♂♂, while the form shown in Sars's (1895) pl. 192, fig. 1 refers to the larger and older. The species key given in Chevreux & Fage (pp. 294–5) therefore requires modification.

Family **Photidae**

MICROPROTOPUS MACULATUS Norman

Salstone 13. v. 49, ♂♂♀♀ breeding.

EURYSTHEUS MACULATUS (Johnston)

Stomachs of *Gadus minutus* in June 1948. Salcombe, Castle Rocks, 12. v. 49, 2♀♀.

PODOCEROPSIS SOPHIAE Boeck

Bottom fauna of L 4, 3. vi. 49, ♂. Stomachs of *Gadus minutus*, in June 1948.

LEPTOCHEIRUS PILOSUS Zaddach

River Tamar, Cothele Ferry, 28. ii. 48, a number of juv. amongst stolons at *Cordylophora lacustris*. Also obtained in the Helford River, W. Cornwall, at head of Frenchman's Creek, Sept. 1949.

Family **Amphithoidae**

AMPHITHOË VAILLANTI Lucas

Plymouth Sound: dredgings from Asia Shoal, 2. vi. 49, ♂♂♀♀.

Family **Podoceridae**

PODOCERUS VARIEGATUS Leach

Salcombe, Castle Rocks, sievings at L.W., 12. v. 49, several ♂♂♀♀.

Family **Caprellidae**

PHTISICA MARINA Slabber

In plenty in stomachs of *Gadus minutus*, 1948, especially in July. Also in stomachs of *Callionymus lyra*, 1949.

Salcombe, Castle Rocks, L.W., one; Salstone, L.W., a few, 13. v. 49.

PSEUDOPROTELLA PHASMA (Mont.)

A few in stomachs of *Gadus minutus* with the above.

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PISCES

By G. A. Steven

Some records are given of fishes, occasional or rare in the area, recently caught in the western part of the English Channel. The nomenclature is that used in the *Plymouth Marine Fauna* (Mar. Biol. Assoc., 1931) based on Duncker, Ehrenbaum, Kyle, Mohr and Schnakenbeck's list in *Die Tierwelt der Nord- und Ostsee* (1925–29). An asterisk indicates species that do not appear in the *Plymouth Marine Fauna*.

Family **Trygonidae**

TRYGON PASTINACA (L.)

One female in trawl on 18. xi. 49 in position Start Point bearing 270°, distant 8 miles.

Family **Myliobatidae**

MYLIOBATIS AQUILA (L.)

One female in trawl on 6. xii. 49 in position Eddystone bearing 115°, distant 6 miles.

Family **Balistidae**

BALISTES CAPRISCUS Gmelin

One caught in lobster store-pot in Fowey Harbour on 8. ix. 49. The pot had been emptied of lobsters the day before and put back in the water with the door open.

Family **Tetrodontidae**

*TETRODON LAGOCEPHALUS L.

One specimen caught by hand in shallow water in Mousehole Harbour (Cornwall) on 21. x. 49. The fish was alive but swimming very feebly and was being attacked by seagulls.

Family **Gadidae**

RANICEPS RANINUS (L.)

One in Agassiz trawl off Plymouth 26. x. 49.

Family **Carangidae**

NAUCRATES DUCTOR (L.)

One in mackerel drift net in position Carn Dhu Point (Cornwall) bearing 010°, distant 24 miles, on 1. vi. 49.

Family **Serranidae**

SERRANUS CABRILLA L.

Five specimens in trawl in position Eddystone bearing 315°, distant 40 miles, on 6. x. 49. One was brought back alive and is still living in the laboratory aquarium.

Family **Sparidae**

CANTHARUS LINEATUS (Montagu)

One in otter trawl off Plymouth on 1. xii. 49. This fish, though rare in the Plymouth area, is not infrequently landed at Newlyn in trawled catches from deeper water on the western fishing grounds.

Family **Scombridae**

EUTHYNNUS PELAMYS (L.)

One specimen, 17 in. long and $2\frac{3}{4}$ lb. weight, caught on 15. ix. 49 in a fixed net in Plymouth Sound.

*SARDA PELAMYS Brünnich

One specimen 20·5 cm. in length caught in Whitsand Bay on 30. ix. 49; another (31·5 cm.) in a pilchard drift net off Rame Head on 23. xi. 49; a third, off Plymouth, also in a pilchard drift net, on 6. xii. 49.

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NOTES ON THE PLYMOUTH MARINE FLORA

ALGAL RECORDS FOR THE PLYMOUTH REGION

By Mary Parke

The greater number of the species given in this list are new records for the Plymouth region. Recent records for some rare species have also been included.

MYXOPHYCEAE

Family **Chamaesiphonaceae**

XENOCOCCUS SCHOUSBOEI Thuret

Wembury, Plymouth; on *Enteromorpha* at M.H.W.N.T.; gonidia in March.

Family **Oscillatoriaceae**

PLECTONEMA BATTERSII Gomont

Plymouth; M.H.W.N.T. zone on rock; March.

CHLOROPHYCEAE

Family **Chlamydomonadaceae**

BRACHIOMONAS SUBMARINA Bohlin

Rame Head; in small pool above E.H.W.S.T.; July.

Family **Polyblepharidaceae**

PYRAMIMONAS GROSSII Parke

In inshore waters off Plymouth during all months of the year.

Family **Chlorodendraceae**

PRASINOCLADUS LUBRICUS Kuckuck

Salcombe, Yealm, Wembury, Plymouth, Looe: M.H.W.N.T. downwards; frequent on stones in pools and on the edges of pools or holes in the rock, also found on shells dredged from 4 m. below M.L.W.S.T.; most frequent in winter and spring but can be found throughout the year; zoosporangia at all times of the year. Recorded from Plymouth (Batters, 1900), Isle of Man (Parke, 1933), Blackpool and Millport (Fritsch, 1949).

Family **Chaetophoraceae**

BOLBOCOLEON PILIFERUM Pringsheim

Wembury: growing on the frond of *Laminaria digitata*; zoosporangia in March.

Epicladia flustrae Reinke

Salcombe, Wembury, Plymouth, Looe: in *Dynamena pumila* growing on *Fucus serratus*; zoosporangia in spring and summer; the form with longer, more slender filaments (var. *phillipsii* of Batters) is usually found in *Alcyonidium hirsutum* growing on *Chondrus crispus* at E.L.W.S.T.; zoosporangia in March.

PHAEOPHYCEAE

Family **Ectocarpaceae**

Giffordia sandriana (Zanard.) Hamel

Plymouth; on raft near breakwater and in tanks at the Plymouth laboratory; unilocular and plurilocular sporangia in spring and summer.

Family **Acinetosporaceae**

Haplospora globosa Kjellman

Plymouth; growing on ropes hanging down from raft near the breakwater; monosporangia in May.

Family **Myrionemataceae**

Endodictyon infestans Gran

Wembury; in *Alcyonidium hirsutum* growing on *Chondrus crispus* at E.L.W.S.T.; plurilocular sporangia in March.

Ascocyclus sphaerophorus Sauvageau

Wembury; on the fronds of *Laminaria saccharina* growing at M.L.W.S.T.; unilocular sporangia in August. Recorded previously from Sidmouth.

Family **Corynophlaeaceae**

Corynophlaea crispa (Harv.) Kuckuck

Looe; on *Chondrus crispus* at M.L.W.N.T.; unilocular sporangia in June and July.

Family **Chordariaceae**

Castagnea zosterae Thuret

Looe; on *Zostera* at M.L.W.S.T.; unilocular sporangia in July.

Mesogloia lanosa Crouan

River Yealm; on sandy ground 1–2 m. below M.L.W.S.T.; unilocular sporangia in July.

Myriocladia lovenii J. Agardh. (?)

Plymouth; on shells and small stones at a depth of 8–10 m. below M.L.W.S.T.; found only from late June to August; unilocular sporangia July and August. The material from Plymouth Sound agrees very closely with the description of

Agardh's Swedish material, but according to Kylin (1933) the plant found on the British coast is not the same as that found on the west coast of Sweden. The British plant may, therefore, have to be placed in a new species.

Family **Stictyosiphonaceae**

STICTYOSIPHON SORIFERUS (Reinke) Rosenvinge

Plymouth; on shells 6–10 m. below M.L.W.S.T.; plurilocular sporangia in July.

Family **Striariaceae**

MYRIOTRICHIA REPENS (Hauck) Karsakoff

Looe: on *Stilophora rhizodes* and *Scytosiphon lomentaria* at M.L.W.S.T.; plurilocular sporangia in July. Recorded previously from Wembury.

MYRIOTRICHIA DENSA Batters

Looe; on *Zostera* at M.L.W.S.T.; unilocular and plurilocular sporangia in July and August. Recorded for River Yealm in 1896.

Family **Sphacelariaceae**

SPHACELARIA FURCIGERA Kützing

Looe: on *Cystoseira ericoides* at M.L.W.S.T.; propagules in July.

Family **Sporochnaceae**

CARPOMITRA COSTATA (Stackhouse) Batters

Eddystone; trawled within 3-mile radius from a depth of 40–50 m. growing with *Dictyopteris membranacea*; unilocular sporangia in August and September. Recorded as growing in Plymouth Sound from 1870–1900, but it has not been obtained from this locality in recent years.

Family **Desmarestiaceae**

DESMARESTIA DUDRESNAYI Lamouroux

Eddystone; one young plant trawled within three-mile radius from a depth of 40–50 m. Previous records from this locality 1894–96.

Family **Laminariaceae**

LAMINARIA OCHROLEUCA De la Pylaie

Plymouth; on rock from M.L.W.S.T. down to depth of 8 m.; fertile from April to November–December. See Spooner, p. 261, for further records.

RHODOPHYCEAE

Protoflorideae

Family **Erythropeltidaceae**

ERYTHROPELTIS DISCIGERA (Berth.) Schmitz var. FLUSTRAE Batters

Lannacombe, Wembury, Plymouth; on *Plumularia*, *Flustra* and *Alcyonidium* from M.L.W.S.T. downwards; gonidia in February and March.

Florideae

Family **Chantransiaceae**

ACROCHAETIUM ENDOZOICUM (Darbyshire) Batters

Wembury; in *Alcyonidium hirsutum* growing on *Chondrus crispus* at M.L.W.S.T.; monosporangia in March.

Family **Naccariaceae**

ATRACTOPHORA HYPNOIDES Crouan

Plymouth; on shells at a depth of 8–12 m. below M.L.W.S.T. growing with *Dudresnaya verticillata*, *Stenogramma interruptum* and *Spondylothamnion multifidum*; cystocarpia in July. Recorded previously from Exmouth.

Family **Grateloupiaceae**

GRATELOUPIA MINIMA Crouan

Dr M. A. Westbrook (Mrs D. P. Wilson) supplies the following. Only previous records Ilfracombe and Torquay (Batters, 1900). Wembury, Church reefs, February 1932; Mewstone reefs, September 1932. Gregarious on the edges of flat stones in shallow pools at L.W.S.T. The tiny plants resembled a mat of sporelings, in colour reddish brown rather than the violet-purple described by Newton (1931); they were unbranched excepting for an occasional dichotomizing tip. The internal structure resembled that of *G. filicina*. Most of the older parts of the February plants were covered with young tetrasporangia.

Family **Squamariaceae**

PEYSSONNELIA ATROPURPUREA Crouan

Wembury; on rock under ledges at E.L.W.S.T.; tetrasporangia in May.

Family **Corallinaceae**

LITHOPHYLLUM HAPALIDIOIDES (Crouan) Heydr. var. *confinis* Foslie

Wembury; M.T.–L.W.N.T. on rock.

Family **Gigartinaceae**

GIGARTINA TEEDII Lamouroux

Salcombe; on mud-covered rocks at E.L.W.S.T. Recorded from Torbay area 1811–88.

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ADDITIONAL RECORDS OF *LAMINARIA OCHROLEUCA* DE LA PYLAIE

By G. M. Spooner

(Plate I)

Laminaria ochroleuca De la Pylaie was recently added to the British flora by Dr Mary Parke (1948), who found it to occur freely in the sheltered parts of Plymouth Sound. It had first come to notice in 1946 and is possibly quite a recent introduction to the country, though it may have escaped notice for some years. The species can now be recorded from two other localities: Salcombe Estuary (South Devon), and Helford River (West Cornwall).

Salcombe, west side of the estuary, first observed 13 April 1949, a few plants round Woodville Rocks, in an area where all four *Laminaria* species and *Sacchoriza bulbosa* De la Pylaie occurred together in the L.W.S. region. Later, on 12 May, a continuous bed observed, exposed at extreme low water, on the north side of Fort Charles Rocks.

Helford River, north shore at level of E. Calamansack, a few single stunted *Laminaria* plants below E.L.W.S., amongst which was one *L. ochroleuca* (the remainder *L. saccharina* Lamour.) 25 September 1949.

Both the new localities happen to be in estuaries, but in neither of the habitats in which the weeds were found can the influence of fresh water be regarded as appreciable. The fauna of each habitat includes echinoderms (at the Helford River site, large examples of *Marthasterias glacialis* (L.) occurred). It is possibly the relative shelter obtainable in these narrow inlets of the sea that is advantageous to this *Laminaria*.

In the early spring of 1949, after an unusually mild winter, there was a rich growth of various littoral brown algae. An extensive bed of *L. ochroleuca* in Rum Bay, Plymouth Sound, was well exposed by the −2 ft. tide of 16 March, and the zonation relative to *L. digitata* Lamour. well demonstrated. The two zones could be seen mixing and the populations overlapping at about M.L.W.S.

level. On the other hand, not a trace of the species could be detected on the reefs off Wembury Point, where *L. cloustoni* Edm. occupies a long stretch of shore in the region of E.L.W.S. and below. Wembury Bay is decidedly more exposed to wave action than is much of the shore inside Plymouth Sound, and a particular instance of extensive destruction of brown algae occurred during a southerly gale on 3 April 1949, as a result of which, many tons of weed were deposited in the upper tidal zone.

Further evidence was thus obtained that *L. ochroleuca* occupies the same bathymetric levels as *L. cloustoni*, which, on the south coast of Devon and Cornwall, it may tend to replace in sheltered habitats. That these two species are in active competition for the same ground where there is moderate shelter seems a fair deduction, and continued observation is desirable to show how far equilibrium between the two species has been reached.

The photograph in Pl. I, taken by Dr D. P. Wilson at Salcombe, serves to show the main features by which *L. ochroleuca* is distinguished in the field from its nearest ally, *L. digitata*.

REFERENCE

PARKE, MARY, 1948. *Laminaria ochroleuca* De la Pylaie growing on the coast of Britain. *Nature*, Vol. 162, p. 295.

EXPLANATION OF PLATE I

A plant of *Laminaria ochroleuca* (centre) growing amongst other oar-weeds, Salcombe, May 1949. A plant of *L. digitata* lies behind it with its stipe on the left side, showing the characteristic prostrate habit when left exposed on the shore. Several fronds of *L. saccharina* also lie prostrate. In the *L. ochroleuca* plant the stiffer stipe is semi-erect and the pronounced pale colouring of the base of the frond is well indicated.

Photo by D. P. Wilson

ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

RICERCHE SU *ASTERINA GIBBOSA* (PENN.). I. LA MIGRAZIONE DELLE GONADI. II. L'ERMAFRODITISMO IN UNO POPOLAZIONE DI PLYMOUTH

By Guido Bacci

Arch. Zool. Ital., Vol. XXXIV, 1949, pp. 23–29, 47–74.

The gonads of *Asterina gibbosa*, in individuals with an arm length of 3 mm., the smallest sizes examined, are still found in the aboral region. During subsequent growth, they turn along the internal walls of the interradial zones until they reach the vicinity of the mouth in the oral position. When this definitive position is reached (in individuals with an arm length of 9 mm. in the Plymouth *Asterina*) the genital pores open.

The great difference in the embryological processes by which analogous conditions are reached in ophiuroids is emphasized.

A. gibbosa is represented by an Atlantic race which has only hermaphrodite individuals and a Mediterranean race which has partly hermaphrodite and partly gonochoristic individuals (Cuenot). In the present work the problems of sex-differentiation and of sex-determination in a wholly hermaphrodite population occurring in the waters of Plymouth Sound are examined both by morphological and statistical methods.

Morphological study of the gonad development has given the following results: (i) the gonads appear ambisexual from a very early stage; (ii) the maturation of the male always precedes that of the female elements which continue their growth during the male phase; (iii) individual differences can be observed in this relative rate of maturation of the male and female elements; (iv) ripe sexual elements left in the gonad after spawning are destroyed by amoebocytes; (v) vesicular tissue formations appear in the gonad both of the male and of the female after spawning; (vi) germinal elements of the ripe gonads in the female phase are represented by female germ cells only; (vii) the absence, during the reproductive period, of transition stages between gonads in the male and in female phases shows that the change from the male to the female phase takes place between successive spawning periods.

A statistical analysis of the sexual phases in the population gives the following results: (i) all the individuals of the population are protandric hermaphrodites; (ii) sex reversal takes place in individuals having an arm length between 9 and 16 mm.; (iii) the maximum rate of change is found to occur in individuals having a size which more or less corresponds to that attained when the males and females are in equal numbers.

The necessity of dividing the study of sex in its morphophysiological (differentiation) and genetical (determination) aspects is emphasized; the existence among Metazoa of species with totally phenotypical sex-determination is considered doubtful.

On the ground of preceding statistical research (Bacci, 1947) and of the results on *Asterina* two main categories in the sex determination of hermaphrodites may be defined. In the first one (*Patella* type) the action of sex factors is exercised with an unequal intensity among the different individuals of a population. In the second (Plymouth *Asterina* type), sexual factors are in a condition of approximate balance among the different individuals of the population. While in the first category sex determination is probably due to multiple factors, in the second, sex determination is certainly due to a gene mechanism. As far as sex differentiation is concerned three principal conditions are considered in hermaphrodite animals. In the first (false gonochorists) each sexual phase contains elements of only one type. In the second, heterologous elements coexist in the same phase but never reach maturation at the same time. In the third, the heterologous elements reach maturity in the same period so that even autofecundity is made possible. For the species of the first two categories of differentiation the following principle is considered to be general. In hermaphrodite animals with distinct sexual phases sex change takes place during the period of sexual rest. G.B.

Some New Myxosporidia from Plymouth with a Proposed New Classification of the Order

Yogendra R. Tripathi

Parasitology, Vol. 39, 1948, pp. 110–18

Four new species of Myxosporidia are described from fishes at Plymouth, *Sinuolinea rebae* n.sp. from the urinary bladder of *Solea solea*, *Leptotheca vikrami* n.sp. from the gall bladder of *Zeus faber*, *Zschokkella russelli* n.sp. from the gall bladder of *Gaidropsarus tricirratus*, and *Ciliata mustela* and *Zschokkella sturionis* from the gall bladder of *Acipenser sturio*. This is the first record of amyxosporidian from a chondrostean. An attempt has been made to standardize the terminology used in describing the spores. The terms as used by Kudo (1920) are adopted because they are well defined and used by many other authors. A new classification is proposed, based on the form of the spores, and an emended definition of the genus *Leptotheca* is given. Y.R.T.

The Function of the Giant Axon of *Myxicola infundibulum* Montagu

By J. A. C. Nicol

Can. Journ. Research, D, Vol. 26, pp. 212–22.

The giant axon of *Myxicola infundibulum* runs throughout the nerve cord and gives off peripheral branches to the longitudinal muscles. Movements of the animal are quick synergic contractions of the whole body and slower metachronous locomotory movements. Injury to the giant axon without interrupting the rest of the nerve cord blocks the passage of the quick contraction but not of slower locomotory waves. It is concluded that the quick end-to-end shortening is intermediated by the giant axon and that slow waves of locomotion depend upon transmission through short segmentally linked neurones. Traction of one segment on another is not effective in transmitting either type of movement. The giant fibre response is of an all-or-none nature. Repetitive stimuli lead to summation of muscular contractions. The axon conducts in either direction during the natural life of the animal. The nature of the effective stimuli, the simplicity of the neuronal arrangement involved, and the character of the synergic response are discussed in terms of their survival value to the species. J.A.C.N.

Conduction Velocity in Relation to Axon Diameter in *Myxicola infundibulum*

By J. A. C. Nicol, C. N. Smyth and D. Whitteridge

XVII Int. Physiol. Congr. Oxford, 1947, pp. 243–4.

Some characteristics of conduction in the giant axon of *Myxicola infundibulum* are presented. The axon tapers from 0·5–1 mm. at one end to 0·1 mm. at the other. A single electrical stimulus leads to a nerve action potential which is all or none. Sharp mechanical stimuli give rise to single nervous impulses resulting in separate muscular contractions. The axon conducts equally well in both directions, when the stimulation is electrical or mechanical. J.A.C.N.

POPULATION-DISPERSION IN *TELLINA TENUIS* DA COSTA

By N. A. Holme, B.A.

Zoologist at the Plymouth Laboratory

(Text-figs. 1–8)

CONTENTS

	PAGE
Introduction	267
Tellina tenuis	268
Description of the habitat	268
Population counts	269
Plots of individuals	270
Natural populations	270
Artificial populations	276
Discussion	279
Summary	280
References	280

Introduction

Although many investigations have been made of soil populations, both in terrestrial and aquatic environments, little is yet known of the distribution of individuals in relation to one another. A study of distribution in the horizontal plane lends itself either to a statistical treatment of samples from adjacent areas, or, where possible, to plotting of individuals *in situ*.

Salt & Hollick (1946) have studied the micro-distribution of wireworms by statistical treatment of eighty-one similar soil samples taken from a square yard of pasture. The wireworms were shown to be non-randomly distributed, there being a tendency for individuals to be aggregated.

In this paper an account is given of a population of the mollusc *Tellina tenuis* da Costa in which distribution is shown to be non-random, tending towards an even distribution. Investigations have been made both by statistical treatment of samples and by plotting of individuals.

Although there is some evidence that populations of this mollusc on other shores are not so distributed, the results from this area seem to be of sufficient general interest to be placed on record.

I am most indebted to Mr G. M. Spooner for assistance with the statistical calculations.

Tellina tenuis

Tellina is a small, thin-shelled, lamellibranch, which reaches a length of about 16 mm. in the Exe estuary. When excavated at low tide the animals are found at depths ranging from 2 to 4 in., smaller sizes usually being nearer the surface. Nearly all the animals are found lying on their sides, in a quiescent state, with neither siphons nor foot protruded.

At high tide, however, the animal probably assumes an upright position with siphons protruded, as shown in Fig. 1. The inhalent siphon is very extensile and ranges over the surface of the sand, drawing in material lying on

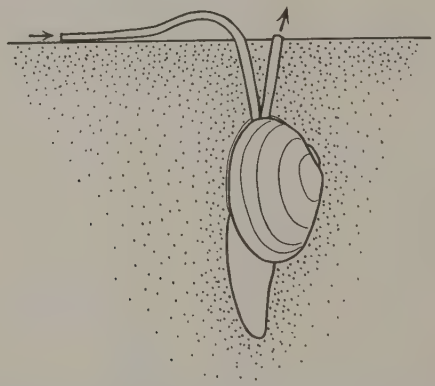


Fig. 1. Position of *Tellina tenuis* in the sand at high tide. After Yonge (1949).

or just above the surface. The shorter exhalent siphon does not project above the surface of the sand (see Yonge, 1949). Prof. C. M. Yonge, F.R.S., informs me that *Tellina* probably makes vertical migrations in the sand, coming nearer the surface at high tide.

Description of the Habitat

The habitat, which has been described by the writer (Holme, 1949), is a sheltered sandy beach within the mouth of the Exe estuary. From about half tide downwards the soil consists of fine clean sand, which slopes down to a small stream known as Salthouse Lake. A bed of clay occurs at a depth of about 2 ft. below the surface, and the sand is consequently not very well drained.

In the lower half of the beach *T. tenuis* and *Arenicola marina* are dominant members of the fauna. *Cardium edule* and *Macoma balthica* occur in small numbers in this region.

The stations referred to are on a traverse from high- to low-water marks.

Stations were at 100 ft. intervals up the beach, heights above M.L.W.S.T. being: Station H, 2 ft.; Station G, 4 ft. (L.W.N.T.); Station F, 6 ft. (half-tide mark); Station E, $7\frac{1}{2}$ ft.

Other stations, indicated in Roman numerals, are at a little above half-tide mark, on a traverse ranging from sand to mud.

Population Counts

On a number of occasions counts have been made of populations of *Tellina* in adjacent areas on the beach. Each time a square metal frame was driven into the sand and the soil inside it excavated to a depth which appeared to include all the fauna. The soil was sieved through a 1 mm. mesh. In 1947, areas of $\frac{1}{4}$ m.^{2} were excavated, but later investigations have been on $\frac{1}{10}$ m.^{2} areas.

If individuals are distributed at random, the counts from separate samples should vary according to a Poisson distribution.

Salt & Hollick (1946) have made use of the 'coefficient of dispersion' when dealing with parallel samples of wireworm populations. It follows directly from the fact that the σ^2 of the Poisson distribution tends to equal the mean in value that the expression

$$\frac{\Sigma(x-\bar{x})^2}{\bar{x}(n-1)}$$

leads to unity when individuals are randomly distributed, to less than unity when they are evenly distributed, and to more than unity when they are aggregated. The significance of the divergence is tested by the formula

$$2\sqrt{\frac{2n}{(n-1)^2}}.$$

Where n, the number of samples, is less than 10, the latter expression is greater than unity, so that samples numbering less than 10 cannot be tested for an even distribution.

July and August 1947 (see Holme, 1949)

Pairs of samples, such as D+3 or D−3 were about 4 ft. $4\frac{1}{2}$ in. apart (6 ft. to their outside edges), and the collections around Station I were within 11 ft. of one another.

Numbers per $\frac{1}{4}$ m.^{2} were:

I−3B	5	E II−3	19	D−3	3	G−3	47
I−3A	4	II+3	22	D+3	3	G+3	47
I+3	7						
I+8	7	III−3	1	F−3	45	H−3	42
		III+3	0	F+3	46	H+3	45
						H+15	48

The results show a general uniformity in density at any one station; also a very even population at Stations F, G and H, which range from low tide up to half-tide mark. The 'coefficient of dispersion' of the 7 samples from these three stations is 0·085. There are too few samples, however, to show a significant result.

20 *October* 1948

Twelve areas of $\frac{1}{10}$ m.^{2} were excavated within a radius of $4\frac{1}{2}$ ft. from Station G. Numbers of *Tellina* in each square were respectively: 27, 25, 24, 28, 26, 26, 32, 31, 32, 24, 29 and 29.

The 'coefficient of dispersion' is 0·307, but this lies within the limits of significance: $1 \pm 0{\cdot}89$.

18 *November* 1948

Four adjacent samples of $\frac{1}{10}$ m.^{2} were excavated at a position 30 ft. north-east of Station F.

Numbers of *Tellina* were 15, 15, 14 and 17 respectively. The 'coefficient of dispersion' is 0·13.

The above sets of readings taken together suggested that the distribution of *Tellina* is non-random, and this is confirmed by results shown below.

Plots of Individuals

Natural Populations

Further information has been obtained by plotting the position of each shell in $\frac{1}{10}$ m.^{2} squares. The frame was driven into the sand, and the soil outside it was then scraped away carefully, a little at a time. As each shell was uncovered its position was plotted, by measuring the perpendicular distance from the 'centre' of the shell to two adjacent edges of the square. It was nearly always possible to locate each shell without disturbing it. The length of each shell, and its approximate depth below the surface, was also noted. Excavation of a square usually took over an hour, and was only practicable in the better drained parts of the beach.

Although the shells occupy a depth range in the soil of about 2 in., their horizontal distribution only has been plotted. No clear correlation has been found between the horizontal spacing of individuals and the depths at which they occur. As it seems possible that the observed distribution is related to the activities of the siphons on the surface of the soil, the omission of any reference to depth seems permissible. In one square the orientation of each shell was noted, but here again there seemed to be little correlation with spacing of the animals. Plots of positions in this square are shown in Fig. 2, and in other squares in which the orientation was not noted in Figs. 4 and 6.

Although the spatial arrangement of individuals appears at first sight to be haphazard, there is, however, a suggestion of a general spacing out of the shells. A measure of this can be made by subdividing the large square into thirty-six

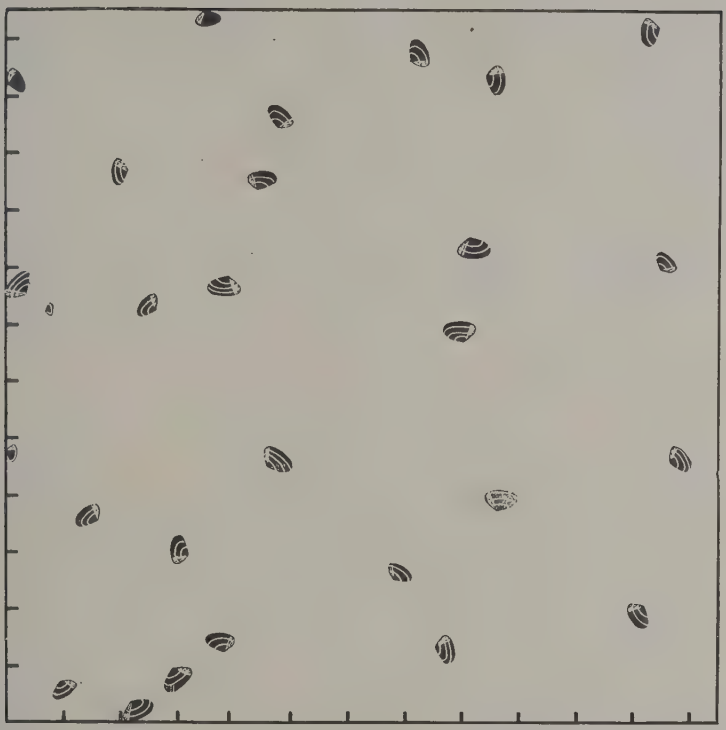


Fig. 2. Plot of positions of *Tellina* in a $\frac{1}{10}$ m.^{2} square (Station F, 11. vii. 49), density 280 per m.^{2} The sides of the square are divided into inches. The shells are drawn approximately to scale, and their orientation is shown by their shaded posterior end. The size and orientation of two shells (top right), shown without rings, is not known.

1	1	1	2	1	1
3	1	0	2	0	0
0	0	1	0	1	1
1	1	0	1	0	1
0	1	0	0	1	1
1	0	1	0	1	0

2

Fig. 3. Distribution of *Tellina* in the square shown in Fig. 2. This has been subdivided into thirty-six squares of side 2 in., the number of animals occurring in each square being indicated.

2 in. squares (Fig. 3), and counting numbers in each square. The $\frac{1}{10}$ m.^{2} areas have a side of *c.* 12·5 in., so that a border of about $\frac{1}{2}$ in. on two sides of the square is neglected.

For example, in the $\frac{1}{10}$ m.^{2} square shown in Fig. 3 the following results were obtained:

No. of individuals	28
No. discarded in margin	2
Mean no. per 2 in. square	26/36 = 0·722

	Frequency	
No. per square	Expected	Observed (f)
0	17·49	14
1	12·63	19
2	4·56	2
3	1·10	1
>3	0·23	0

$\sigma^2 = (19 + 8 + 9 - 18\dot{7})/35 = 17\dot{2}/35 = 0{\cdot}492$
Coefficient of dispersion = 0·492/0·722 = 0·68

The frequencies expected from a random distribution are calculated from the Poisson series.

There is a tendency for a greater number of squares to contain one individual than would be expected from a random distribution.

The coefficient of dispersion is 0·68, which is not, however, significant. The level of significance is $1 \pm 0{\cdot}485$.

Eight other squares (shown in Table I) have been treated similarly, the coefficients of dispersion being: 0·73, 0·59, 0·78, 0·78, 0·82, 0·74, 0·87 and 0·51, the last only being significantly low. If these readings are combined the test of significance becomes $1 \pm 0{\cdot}485/\sqrt{9} = 1 \pm 0{\cdot}16$. The mean of the nine readings is 0·72, so taken together the results show a significant degree of uniform dispersion in the population.

A further, and more revealing, method of showing the spreading tendency of the shells is obtained by plotting the distance of each individual from its nearest neighbour. Inevitably a number of shells are found closer to the edge than to their nearest neighbour within the square, and this tends to leave a fairly substantial residue of shells in which the minimum distance is unknown. Since it is intended to show that individuals do not occur close together, this procedure would leave an element of doubt in the results. This has been overcome by marking a marginal strip round the sample area, of width 1 in., in which the shells are to be neglected, except in their capacity as neighbours. That is, the shells lying in the margin do not contribute a 'minimum distance' reading: they are, however, available when 'minimum distances' for shells in the inner square are being measured (Fig. 4).

The only distances still in doubt are those of shells in the inner square which are nearer to the outer edge than to any other shell. These must, however, be at least 1 in. from their nearest neighbour.

The results of the minimum-distance measurements for the nine squares are shown in Table I. It will be seen that there is a tendency for individuals seldom to occur closer than 1 in. apart, and none was found closer than 0·6 in.

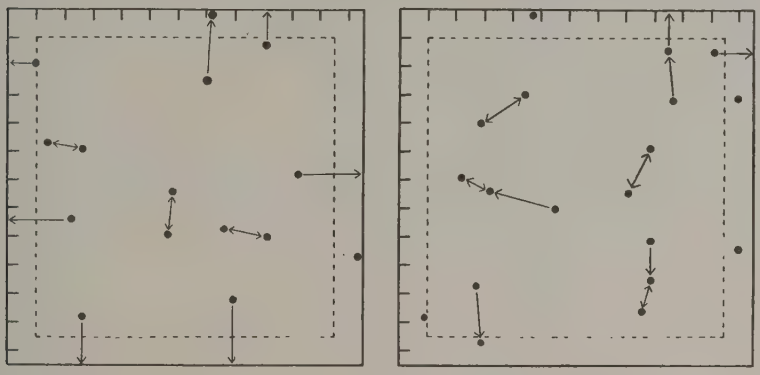


Fig. 4. Plot of positions in two $\frac{1}{10}$ m.² squares, showing the method of measuring minimum distances. A, 30 ft. north-east of station F, 18. xi. 48, density 150 per m.² B, Station F, 3. xi. 48, density 190 per m.².

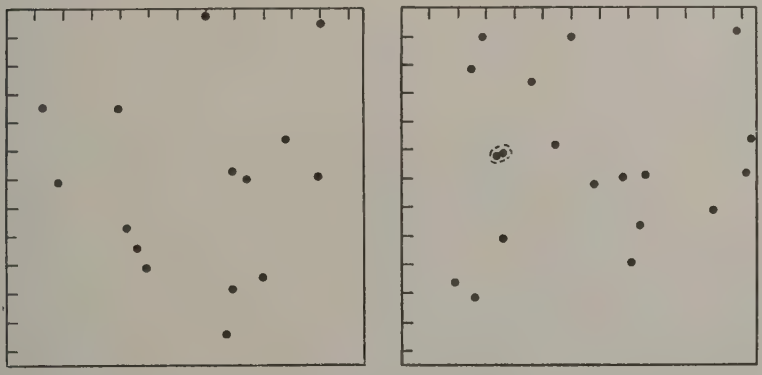


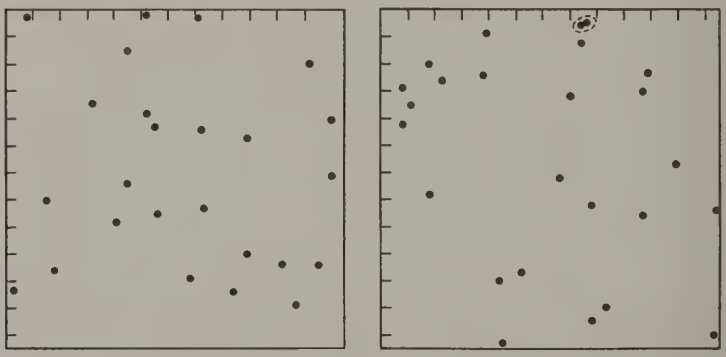
Fig. 5. Randomly distributed points in two $\frac{1}{10}$ m.² squares, for comparison with Fig. 4. Points less than 0·6 in. apart are enclosed by dashes. A, density 150 per m.² B, density 190 per m.²

from its neighbour. That this lower minimum distance is not due to the space occupied by the shell itself is shown by subsequent results (p. 278) in which individuals occurred as close together as 0·1 in. Since the shells occupy a zone of 2 in. depth there seems to be no *a priori* reason why two should not occupy the same position in the horizontal plane, one above the other.

In interpreting the results it should be noted that where two shells are close to one another, the distance between them is often recorded twice, once in respect of each shell.

For comparison, plots have been made of points within 'random squares', the co-ordinates of each point being derived from a table of random numbers. It will be seen that minimum distances below 1 in. occur more frequently in these random squares than in natural populations (Figs. 5 and 6B; Table I).

Mr G. M. Spooner has evolved a formula by which the 'minimum distances' to be expected in a randomly distributed population may be derived. Given P, the frequency of the object or event, the mean minimum distance is shown to be $0{\cdot}5/\sqrt{P}$. Minimum distances will tend to be distributed asymmetrically with a mode at $0{\cdot}3989/\sqrt{P}$. The probability of any one value of x (the minimum distance) being exceeded is $\epsilon^{-x^2\pi P}$.



A B

Fig. 6. Plots of positions in a $\frac{1}{10}$ m.^{2} square of density 250 per m.^{2}, compared with a 'random square'. A, Station G, 3. xi. 48. B, random square.

In this way it has been possible to calculate the number of 'minimum distances' to be expected under 0·95 and 0·55 in. respectively, assuming a random distribution.

Thus, in the square shown in Fig. 2, there were twenty-eight animals ($P = 1/5{\cdot}54$ in.^{2}), seventeen of which were within the 1 in. border. The probability of minimum distances exceeding 0·55 in. is calculated to be 0·8422, and $1 - 0{\cdot}8422 = 0{\cdot}1578$ are therefore expected below 0·55 in. Since seventeen animals occur, the number of minimum distances to be expected below 0·55 in. is $17 \times 0{\cdot}1578 = 2{\cdot}68$. In the same way a minimum distance of less than 0·95 in. has an expected frequency of 6·82.

Comparisons of expected and actual minimum distances are given in Table II. There is seen to be a tendency for minimum distances below about 1 in. to be eliminated by the spacing out of individuals.

Table I. Minimum Distances between Individuals in Natural Populations, Compared with those in the 'Random Squares' Shown in Figs. 5A, 5B and 6B.

The column marked 'others at least 1·0' refers to those shells in the inner square which are nearer the outside edge than to their nearest neighbour inside the square. The column marked 'Discarded, in border' refers to those in the outer border, whose minimum distances are not measured. Note that relatively more distances below 1·0 in. occur in the random squares.

			Minimum distance, in inches																		
Position	Date	Density ($\frac{1}{10}$ m.^{2})	>2·0	2·0	1·9	1·8	1·7	1·6	1·5	1·4	1·3	1·2	1·1	1·0	Others at least 1·0	0·9	0·8	0·7	0·6	0·5	<0·5	Discarded, in border
G	3. xi. 48	25	1	—	—	1	4	2	4	2	—	—	—	—	3	—	—	—	2	—	—	6
F	3. xi. 48	19	2	—	2	4	—	1	—	—	—	2	2	—	1	—	—	—	—	—	—	5
30′ N.E. of F (i)	18. xi. 48	15	3	—	—	—	—	—	4	—	—	2	—	—	4	—	—	—	—	—	—	2
30′ N.E. of F (ii)	18. xi. 48	15	4	—	—	—	—	2	—	—	—	—	—	—	2	—	—	—	—	—	—	7
30′ N.E. of F (iii)	18. xi. 48	14	4	1	—	2	—	—	—	—	—	—	—	—	4	—	—	—	—	—	—	3
30′ N.E. of F (iv)	18. xi. 48	17	3	—	1	—	—	2	—	—	—	—	2	—	5	—	—	—	—	—	—	4
F	11. vii. 49	28	2	—	—	1	—	2	1	2	—	2	—	1	6	—	—	—	—	—	—	11
6′ S. of F	11. vii. 49	21	3	—	—	2	—	—	—	—	3	—	—	—	2	—	2	1	2	—	—	6
G+75	11. vii. 49	19	4	—	1	2	2	—	2	—	—	—	1	—	3	—	—	—	—	—	—	4
Total		173	26	1	4	12	6	9	11	4	3	6	5	1	30	—	2	1	4	—	—	48
Random (Fig. 5A)	—	15	1	—	—	1	—	—	—	—	—	2	—	—	4	—	3	—	2	—	—	2
Random (Fig. 5B)	—	19	2	—	—	1	—	—	—	—	2	1	1	—	3	2	2	—	—	—	2	3
Random (Fig. 6B)	—	25	—	1	1	—	—	—	3	—	—	—	—	—	2	2	2	6	—	—	—	8

Table II. Table of Expected and Observed Minimum Distances for the Squares Shown in Table I.

		1·00 in. or over		0·95–0·60 in.		0·55 in. or under	
Density	In border	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.
25	6	12·03	17	4·27	2	2·70	—
19	5	9·78	14	2·63	—	1·59	—
15	2	9·79	13	2·03	—	1·18	—
15	7	6·03	8	1·24	—	0·73	—
14	3	8·52	11	1·58	—	0·90	—
17	4	9·43	13	2·24	—	1·33	—
28	11	10·18	17	4·14	—	2·68	—
21	6	10·21	10	2·98	5	1·81	—
19	4	10·48	15	2·82	—	1·70	—
	Total	86·45	118	23·93	7	14.62	0

Artificial populations

If the population density is increased the chances of randomly distributed individuals coming to lie close together becomes greater. Two experiments have been made in which individuals were concentrated within a metal circle from which they could not escape. After a period of several weeks a $\frac{1}{10}$ m.^{2} area within the circle was excavated and positions of the shells plotted.

Experiment I

The metal circle was made from a strip of sheet steel 6 ft. long and 6 in. wide, which was bent into a circle of diameter *c.* 22 in., and the ends joined. The circle was pushed into the sand until its top was level with the surface.

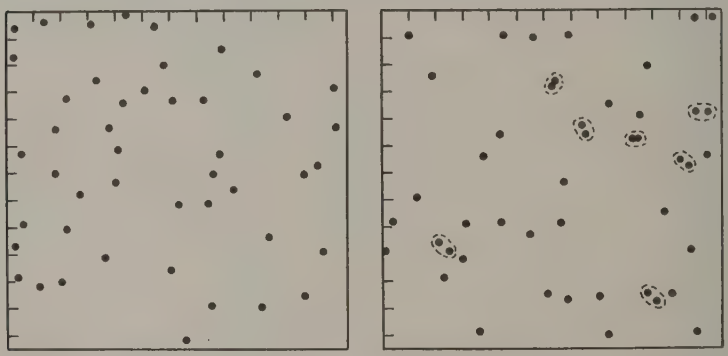


Fig. 7. A, plot of positions in a $\frac{1}{10}$ m.^{2} square of artificially high density (Exp. I), 30. iii. 49, density 460 per m.^{2} The animals have dispersed from a point just outside the top left-hand corner. B, random square of the same density.

The position chosen was 15 ft. north-east of Station F, where there is a fairly well drained sand supporting a small natural population of *Tellina*. About 100 specimens of *Tellina*, of various sizes, were sieved from sand near low-water mark and placed in a small pit near the edge of the enclosed area. They were then covered over with sand and left for 8 weeks, when a $\frac{1}{10}$ m.^{2} square was excavated. Forty-six shells were found, their positions being shown in Fig. 7A.

The pit in which the shells were originally placed is just outside the square, at the top left-hand corner in the figure, and it will be seen that the population density is higher towards this corner. Examination of the area where the shells had been introduced revealed quite a number which had not yet spread out.

Dividing the large square into thirty-six smaller squares, a coefficient of dispersion of 0·43 is obtained, which is significantly different from unity.

Plots of minimum distances gave the following results:

	Artificial population	Random square
Density	46	46
No. in outer margin	14	11
No. 1 in. or more from edge	2	2
Minimum distances (in.):		
<0·5	—	14
0·5	—	—
0·6	2	1
0·7	—	3
0·8	2	—
0·9	5	1
1·0	3	3
1·1	3	—
1·2	5	6
1·3	2	1
1·4	1	—
1·5	—	1
1·6	3	—
1·7	1	1
1·8	1	1
1·9	—	1
2·0	2	—
>2·0	—	—

These results may be summarized thus:

	Density	In border	1 in. or over	0·95–0·6 in.	<0·55 in.
Artifical population	46	14	23	9	0
Random square	46	11	16	5	14
Expected (from formula)	46	[14]	15·23	9·73	7·04

Spacing-out is shown by the absence of individuals below 0·55 in. rather than in reduced numbers between 0·95 and 0·6.

The results of this experiment show that individuals can spread out and take up their characteristic arrangement in the adult stage, and in a fairly short space of time.

After excavation, most of the shells were returned to the circle, and covered over. A $\frac{1}{10}$ m.^{2} square was again excavated $3\frac{1}{2}$ months later, only twenty-eight specimens being taken.

'Minimum distance' measurements were as follows:

Density		28	
No. in outer margin		7	
No. 1 in. or more from edge		1	
Minimum distances:			
in.		in.	
<0·5	2	1·3	2
0·5	—	1·4	—
0·6	—	1·5	1
0·7	2	1·6	1
0·8	—	1·7	6
0·9	2	1·8	—
1·0	1	1·9	—
1·1	2	2·0	—
1·2	1	>2·0	—

This square is the only one so far in which individuals have been found less than 0·5 in. apart. The general arrangement is otherwise as in natural populations.

Experiment II

About 200 specimens of *Tellina* were placed within a smaller circle, diameter 17 in., close to the previous position. The specimens were scattered over the surface of the sand and covered over. An attempt was made to excavate $4\frac{1}{2}$ weeks later, but this had to be abandoned owing to rain, which started to fill the hole. Only eleven specimens had been removed and these were replaced in the circle.

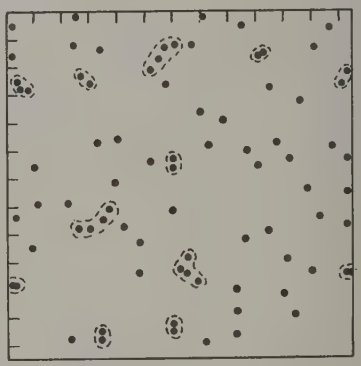


Fig. 8. Plot of positions in a $\frac{1}{10}$ m.^{2} square of artificially high density (Exp. II), 13. vi. 49, density 810 per m.^{2} Note that in thirty-one cases animals occur closer than 0·6 in. apart.

Eight weeks from the start of the experiment, a $\frac{1}{10}$ m.^{2} square was successfully plotted (Fig. 8). The density was eighty-one and when the square was subdivided into thirty-six 2 in. squares, seventy-four were contained within them. The coefficient of dispersion is 0·54, which is just within the limits of significance.

Measurements of minimum distance, however, show that the characteristic spacing found at lower densities had not been assumed:

Density		81	
No. in outer margin		25	
No. 1 in. or more from edge		1	
Minimum distances:			
in.		in.	
<0·5	20	1·0	6
0·5	1	1·1	3
0·6	2	1·2	0
0·7	2	1·3	2
0·8	9	1·4	0
0·9	9	1·5	1

The formula gives 21·93 individuals below 0·55 in., and 21·36 between 0·95 in. and 0·6 in., which is very close to that attained by the animals in this experiment.

Thus in this square the animals are spread rather evenly, judged by information obtained by subdividing the large square; but are distributed at random as shown by minimum-distance measurements. The even distribution is probably explained by the animals being spread out at the start of the experiment, and is of little consequence.

The absence of any tendency to spread out from one another is remarkable, and shows that the 'minimum distance' shown in previous results does not limit the density in an upward direction. Observations on dense natural populations are needed to confirm this break-down of the 'minimum distance' at higher densities, but in view of the constancy of results on previous occasions the results of the last experiment cannot be disregarded.

The occurrence of animals as close together as 0·1 in. shows that the minimum distance is not controlled by the size of the shell itself, but may be the result of some aspect of the animal's behaviour.

Discussion

Aggregation in a population can be quite easily shown by statistical treatment of a very few samples. If any two are widely divergent, aggregation can be shown to occur. On the other hand, an even distribution can only be shown by a much larger number of samples, and any small errors in technique will tend to make the figures approach random.

The results obtained with *Tellina* show that a significant degree of 'over-dispersion' or evenness of the population does occur. This over-dispersion applies to individuals occurring in any one small area, and also to populations extending from low tide up to half-tide mark on the beach in question.

One aspect of this distribution is shown by measuring the distance of each animal to its nearest neighbour. In natural populations it is shown that fewer than would be expected occur less than 1 in. apart, and none occur less than 0·6 in. apart. Where populations on the shore were artificially increased the same type of spacing was shown at a higher density (460 per m.^{2}), but not at a density of 810 per m.^{2} As the density increases the chances of randomly distributed individuals lying close to one another is increased, so that at a density of 460 per m.^{2} a result significantly different from random has been obtained.

It is possible that at moderate densities each individual occupies a territory delineated by the activities of the inhalent siphon on the soil surface, but that at higher densities the spacing breaks down owing to the confusion resulting from a number of siphons meeting one another on the surface. Thus the 'territory', if there be one, would seem not to limit density. This is supported by observations of Stephen (1928–30), who found populations as high as 7588 per m.^{2} in Kames Bay. Examination of Stephen's data shows no evidence of uniform populations either at any one place or over a stretch of shore, as occurs in the Exe. In fact, Stephen (1930) has emphasized the variability in populations at any one place. He excavated four $\frac{1}{4}$ m.^{2} areas within a few yards of each other at St Andrews and found the following numbers in each: 114, 136, 111 and 163 respectively. These show a coefficient of dispersion of 4·4, which indicates a significant degree of aggregation. It is

possible, however, that there may have been drainage or other differences in conditions between the four areas.

Although the even distribution in the Exe might be due to an even spat settlement, the results with artificially increased populations indicate that the spacing can be taken up in the adult stage. It is not at all clear, however, how such an even spacing over a distance of 215 ft. up the shore has occurred.

Certain other lamellibranchs, notably *Macoma*, *Abra* and *Scrobicularia* have a similar mode of life to *Tellina*; and it would be of interest to examine their distribution where they occur in fairly dense beds.

Summary

A population of the lamellibranch *Tellina tenuis* in the Exe estuary is shown to be uniformly distributed, indicating a significant degree of 'over-dispersion'.

By plotting the position of each shell in squares of $\frac{1}{10}$ m.^{2} area it is shown that fewer individuals than would be expected occur less than 1 in. from their nearest neighbour, and none occurs closer than 0·6 in.

When the population density was artificially increased on the shore the same characteristic spacing was found at a moderate density, but not at a rather higher density.

It is suggested that spacing is correlated with the foraging activities of the inhalent siphon on the soil surface.

Very dense populations have been found by Stephen in other areas, indicating that the size of the 'territory' does not limit density. His results show no evidence of the same phenomena as observed in the Exe.

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GREGARIOUSNESS DURING SETTLEMENT IN THE BARNACLE *ELMINIUS MODESTUS* DARWIN

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(Text-figs. 1–3)

CONTENTS

	PAGE
Introduction	281
Methods	284
Preliminary small-scale experiment	285
Critical small-scale experiment	287
Comparison between settlement on plates exposed in muddy areas, where barnacles were absent, and in neighbouring shelly areas, where barnacles were numerous	291
Gregariousness as a factor affecting the distribution of *Elminius*	295
Summary	295
References	296

Introduction

Many species of marine animals have been described as local or gregarious. Jeffreys (1863–9) and Eales (1939), for instance, made occasional use of the latter term. It implies crowding, often in a restricted habitat, usually in a search for food or shelter. Such crowding must facilitate breeding. Thorson (1946) reviewed the evidence that even non-copulatory species are stimulated to spawn by crowding, and quoted a few observations suggesting that certain forms specifically seek the company of their fellows. In the present account the term gregariousness will be reserved for such behaviour, rather than for automatic crowding in restricted habitats.

Thorson also reviewed the gradually accumulating evidence that the settlement of marine larvae at the end of their planktonic phase is generally not haphazard. The idea of 'hit-or-miss' settlement advanced, for instance, by Colman (1933), for several species, including barnacles, is now out of date. Surprising powers of discrimination have been revealed in certain forms, but up to the present time, so far as we are aware, the only larvae shown to be gregarious during settlement are those of the oyster, *Ostrea edulis*. This was demonstrated by experiments in the oyster-breeding tanks of the Ministry of Agriculture and Fisheries at Conway (see Cole & Knight-Jones, 1949). In those experiments, two or three times as many larvae attached themselves to shells which already bore recently settled oyster spat, as to similar shells from

which all previously settled spat had been removed with the point of a needle. This happened consistently, day after day. In general, most larvae attached themselves to those shells which bore most spat, up to a density of from 50 to 100 spat per shell. Once this density had been reached they settled apparently at random upon the more and the less crowded shells, but much less readily on the bare ones. The gregarious tendency was most marked when the spatfall was light. When numerous larvae were settling they quickly covered both spat-shells and bare shells alike.

Spärck's (1949) observations in the Limfjord tended to confirm that oysters are gregarious during settlement, 'since restocking only took place in any considerable degree in places where the density of the left native stock was fairly great and since the continued restocking slowly spread from these places'. Gregariousness was found to be of great importance on Essex oyster beds, where several small widely separated areas were selected and heavily stocked (Knight-Jones, 1949). The subsequent spatfall was much more heavy on these areas than on neighbouring ground where oysters were sparse or absent. It is most unlikely that these arbitrarily selected areas were more suitable for settlement because of such factors as the nature of the bottom or exposure to tidal currents. Some of them were unproductive when unstocked but became productive when stocked. It is highly probable that the heavier settlement upon them was due to the gregarious tendency demonstrated by the critical experiments in the Conway tanks.

Lest it seem incredible that small, simply organized, planktonic larvae should be capable of such behaviour, it may be explained that the mechanism of gregariousness in *O. edulis* need not necessarily be very complex. Larvae which have reached the stage at which they are ready to settle crawl, by means of a ciliated and very mobile foot, upon any substratum with which they may happen to come into contact (Cole & Knight-Jones, 1939). After crawling for a period they usually swim off again. Their discriminatory powers suggest that they can to some extent postpone attachment until they happen to find a place particularly favourable for it. In Essex creeks tidal currents carry swimming larvae several miles in a few hours, enabling those ready to settle to visit a variety of widely separated places. It appears that the presence of other oysters is one of the factors which encourage settlement. The stimulus may perhaps be olfactory, but there is no evidence on this point from work on oysters. On the other hand, laboratory experiments on ascidian larvae (Grave & Nicoll, 1940; Grave, 1941) showed that metamorphosis was hastened by crowding and also by aqueous extracts of larvae, later developmental stages, and adult tissues. It may therefore be expected that ascidian larvae will prove to be gregarious during settlement, stimulated by the water-borne secretions of their fellows, but direct evidence of this has not yet been obtained in the field, so far as we are aware, though it is a matter of common observation that adult simple ascidians usually occur in clumps.

Gregariousness during settlement must be of great biological importance to a sessile form, such as the oyster, in facilitating breeding. Moreover, the individual is likely to find, in a situation where the species is already established, suitable conditions for its own survival.

In the Burnham-on-Crouch district the most serious competitor of newly settled oyster spat is the barnacle *Elminius modestus*, a recent immigrant from the Antipodes (Knight-Jones, 1948). Smooth slates, which were exposed for weekly periods during the summers of 1947, 1948 and 1949 to record the settlement of oyster larvae, were usually covered with these barnacles in a few days. When settlement was very intense the distribution of the barnacles over the surface of a slate was remarkably even. When settlement was light the barnacles tended to settle first in groups but, as colonization of the surface proceeded, the later arrivals rarely settled amongst the grouped individuals but rather upon the bare areas in between the groups. In this way their distribution gradually became even, provided the light settlement was sufficiently prolonged. Like many other barnacles *Elminius* settles particularly abundantly in scratches or irregularities of the surface, but the test-slates used were smooth, and the initial formation of the groups generally appeared to be unrelated to surface irregularities. The impression gained was that the early arrivals on the bare surfaces were gregarious but that the later arrivals on the crowded surfaces tended to space themselves out. Another point which appeared significant was that slates exposed at certain places consistently caught very few barnacles, though settlement elsewhere was very intense and cyprids were abundant in all plankton samples. The only feature which these places appeared to have in common was a bottom of bare mud, from which barnacles were absent. The slates on which settlement was heavy were from places where the bottom was covered with shells, on which *Elminius* was abundant. It seemed possible that gregariousness might have been responsible for the differences observed.

There is plenty of evidence suggesting that settling barnacles have considerable powers of discrimination. The literature is too lengthy to review here, but it seems particularly relevant to note that Visscher (1928) observed cyprids of *Balanus improvisus* and *B. amphitrite* crawling over the substratum for distances of more than 12 mm. and periods of over an hour, apparently testing different areas in a search for a place for attachment. *B. amphitrite* had been observed to attach within 7 days after hatching, yet Visscher kept some cyprids of this species under observation for 10 or 11 days. By then some had attached but many were still active, which suggests that metamorphosis in this species can be delayed if conditions are unfavourable for attachment. One of us (E. W. K. J.) has observed that cyprids of *B. balanoides*, which had been attached anteriorly to the side of a glass vessel and dislodged by a jet of water from a pipette, were capable of swimming about and then attaching themselves again. Burton (1949) wrote 'the first settled larvae (of *Balanus*) seem to attract others to settle in the same spot'. Dr D. J. Crisp and Dr P. N. J. Chipperfield, with whom we had the

good fortune to discuss this subject, kindly informed us that field observations had led them to suppose that barnacles might well be gregarious, but that they had also observed that barnacles often settled alongside surface projections, as though the cyprids had been sheltering there from currents. The tendency to settle in groups upon a uniform surface might therefore be due wholly to the later arrivals obtaining some shelter amongst previously settled barnacles. If so it could not accurately be described as gregariousness.

This point is of considerable practical importance in oyster research. The extremely productive French oyster industry is based on the use of artificial collectors for spat (see, for instance, Dalido, 1948). Experiments with such collectors in Essex creeks have shown promising results, and the chief factor militating against their successful use there is the overwhelming prolific *Elminius*. Critical tests for gregariousness in *Elminius* were therefore carried out, with the positive results recorded here, as part of a study of its settlement behaviour. Further work will be directed towards finding out how far the smothering of collectors by barnacles can be delayed by placing them far from shelly shores where the barnacles are abundant. It is also hoped to offer for publication later some information regarding the spacing-out tendency on crowded surfaces.

It would be interesting to carry out critical experiments on other barnacles. Should a gregarious habit prove general it would have a bearing on the problem of ships' fouling, for it might prove worth while to take special measures for the cleaning of docks and wharves. Without gregariousness this would appear to be useless so far as organisms with lengthy planktonic stages are concerned.

Methods

Small concrete slabs were prepared, each of which held a pair of rectangular plates of smooth glass (Fig. 1). The plates, which measured $23{\cdot}8 \times 13{\cdot}3$ cm., were held on each side by a long coach-bolt, the head of which was embedded in the concrete. They rested horizontally upon the nuts of the bolts, 4 cm. above the upper surface of the slab, and were secured by rubber washers, cut from pressure-tubing. Wire hoops protected the plates and served as carrying handles.

For the small-scale experiments the slabs were buoyed and placed close together below L.W.E.S.T., near Burnham. For the comparison between settlement on muddy and shelly shores they were placed at L.W.O.T., near Paglesham. They were exposed for short periods during late July, August and September 1949. By then the main settlement of *Elminius*, which had occurred as usual during June and early July, was over. Settlement during the period of the experiments was moderate or sparse. In this respect conditions were ideal for testing for gregariousness, in that the spacing-out tendency observed at times of heavy settlement (see above) scarcely came into effect.

A wire counting-frame and a hand-lens were used for counting. In the small-scale experiments counts were made of the barnacles which had settled on certain areas of the plates, details of which are given below and on p. 289. We have not yet learned to distinguish the earliest settled stages of *Elminius modestus* from those of *Balanus improvisus*, which they resemble in size, but we are confident that the results presented here relate to *Elminius modestus*, since plates exposed at the time of these experiments and under similar conditions, but for longer periods, became covered with the characteristically shaped *Elminius*, amongst which were very few *Balanus improvisus*. Over 99% of the barnacles settling at this time on test plates on or near the shore were *Elminius*.

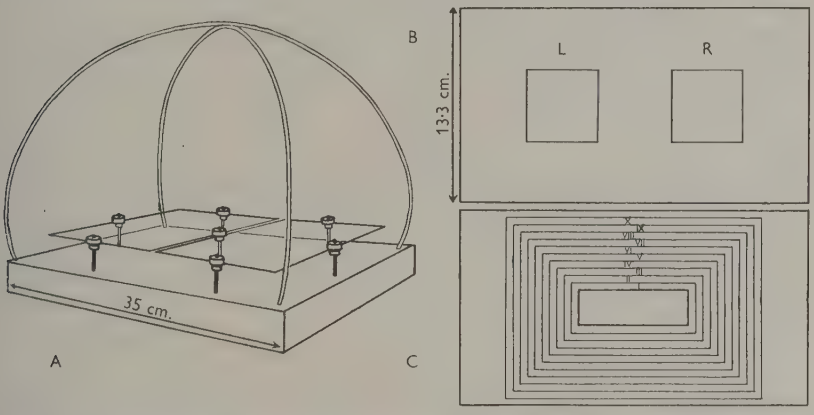

Fig. 1. A, concrete slab, with protecting wire hoops, holding a pair of rectangular glass plates; B, plate marked with areas 5 cm. square, L and R, for preliminary small-scale experiment; C, plate with microscope slide stuck to it. These were exposed in pairs, one with the slide barnacled, the other with the slide bare. When counting the barnacles which settled subsequently, each plate was placed over graph paper marked with the rectangles I–X, and the numbers settling on each narrow area at gradually increasing distances from the slide were obtained. Mean densities on these areas are shown in Fig. 2.

Preliminary Small-scale Experiment

Two areas, 5 cm. apart and each 5 cm. square, were drawn with a diamond on each of four glass plates and marked respectively L and R (left and right, see Fig. 1 B). The plates were placed in position with the side which had been scratched by the diamond downwards. This orientation was adopted because it had previously been found that settlement on glass plates was much heavier on the upper than the lower surfaces. It was therefore decided to use the upper surfaces for small-scale experiments and it was desirable that this experimental surface should be uniformly smooth, since barnacles tend to settle in scratches and may well discriminate between scratches of various depths. The scratches delimiting the experimental squares could be clearly seen through the glass.

The two slabs bearing the four plates were exposed to settling barnacles for a day. The entire lower surface of each plate and all the upper surface except for one of the 5 cm. squares was then wiped with clean cotton-wool. The number of barnacles left in the square was counted and the remainder of the plate was examined to ensure that no barnacles had been left upon it. The plates were exposed for another day, the two slabs being placed near to one another.

TABLE I. SETTLEMENT OF *ELMINIUS MODESTUS* ON PAIRS OF AREAS 5 CM. SQUARE

Areas, 5 cm. square, L and R, marked on glass plates A, B, C and D. Of each pair one area was initially bare whilst the other bore a recorded number of barnacles. The increment on the barnacled area was generally considerably greater than the number settling on the bare area. Most of the exceptions to this rule (marked × in the last column) appear to have been due to mortality amongst the previously settled barnacles exceeding, in the later stages of the experiment, the sparse settlement on the plates.

Period of exposure	Plate	Initial no.		Final no.		Settlement		Ratio Barnacled : bare	
		L	R	L	R	Barnacled	Bare		
21–22. vii	A	—	131	152	595	464	152	3 : 1	
	B	—	140	22	263	123	22	5·6 : 1	
	C	132	—	271	35	139	35	4 : 1	
	D	177	—	471	82	294	82	3·6 : 1	
22–23. vii	A	152	—	241	15	89	15	5·9 : 1	
	B	—	149	7	164	15	7	2·1 : 1	
	C	—	35	12	138	103	12	8·6 : 1	
	D	—	82	2	138	56	2	28 : 1	
23–25. vii	A	—	15	81	64	49	81	1 : 1·7	×
	B	7	—	10	3	3	3	1 : 1	×
	C	12	—	11	1	(−1)	1	—	×
	D	—	48	3	61	13	3	4·3 : 1	
25–26. vii	A	—	64	16	60	(−4)	16	—	×
	B	10	—	21	4	11	4	2·7 : 1	
	C	11	—	59	15	48	15	3·2 : 1	
	D	—	51	7	148	97	7	13·9 : 1	
26–27. vii	A	—	60	26	73	13	26	1 : 2	×
	B	21	—	17	4	(−4)	4	—	×
	C	59	—	127	4	68	4	17 : 1	
	D	6	—	4	7	(−2)	7	—	×
27–28. vii	A	26	—	30	3	4	3	1·3 : 1	
	B	17	—	Plate lost					
	C	127	—	99	10	(−28)	10	—	×
	D	—	7	10	28	21	10	2·1 : 1	

At the beginning of this period each plate therefore presented to settling barnacles two similar squares, one of which was bare whilst the other contained a known number of barnacles. The object of the experiment was to compare the settlement on these squares. At the end of the day the number of barnacles on each square was counted. The results for this and subsequent days are given in Table I.

After counting, each plate was again wiped bare except for one of the squares, which was left barnacled. On a few occasions some of these barnacles were removed, with the object of making subsequent counting easier, and the number

on the square recounted. The plates were then exposed for a further period. Where practicable the square left barnacled was that which had been wiped clean on the previous day. The number of times this change between the two squares L and R was effected for each of the plates can be deduced from Table I, where the plates are designated A, B, C and D.

Table I shows that, in general, settlement was much heavier on the squares which were initially barnacled than on those which were initially bare. A total of 1610 barnacles settled upon the former, 521 on the latter. During the first 2 days, when the initial numbers on the barnacled squares were fairly large and settlement was moderate, the ratios were consistently in favour of the barnacled squares. Later, when the initial numbers were smaller and settlement sparser, inconsistencies appeared, but even some of these supported the idea that the settling barnacles were gregarious. For instance, of the eighty-one barnacles which settled on the bare area of plate A on 23–25 July, sixty-nine settled in a small cluster in a corner of the square. In half of these inconsistencies the final number of barnacles on the barnacled square was less than the initial number, showing that mortality amongst settled barnacles was exceeding settlement. We have often seen evidence of mortality amongst young *Elminius*, and we are inclined to think that most of the inconsistencies in Table I were due to the mortality amongst the relatively large numbers of previously settled barnacles being great compared with the rather small numbers of new arrivals. Giving due weight to this point it is concluded that the squares which initially bore barnacles were considerably more favourable for settlement than those which were bare. This is not indisputable evidence for gregariousness. First, it does not answer the question whether the effect may not be due to mere sheltering amongst the previously settled barnacles, as amongst surface irregularities, and secondly, the bare surface was wiped immediately before exposure, whilst the barnacled surface had not been wiped for 1 or 2 days. Settling larvae of several forms have been shown to favour surfaces covered with bacterial or diatomaceous films (for references see Miller, Rapean & Whedon, 1948; Cole & Knight-Jones, 1949) and such films are acquired after short periods of immersion, though it is doubtful whether one affecting appreciably the behaviour of cyprids would be acquired in such short periods as a day or two.

Critical Small-scale Experiment

A better experimental technique was derived from the account of settlement in *Tubularia* by Pyefinch & Downing (1949), who set a glass microscope slide which bore a colony of *Tubularia* in the centre of a wooden panel and hung it from a raft which itself bore practically no *Tubularia*. A control exposure consisting of a bare slide set in the middle of a similar panel was immersed close beside it at the same time. Much heavier settlement subsequently occurred on the panel to which the *Tubularia* colony was attached (although

this suggests gregarious behaviour it may have been due solely to larvae from the colony settling immediately after liberation).

Accordingly glass slides measuring 2·6 × 7·5 cm. were stuck with 'Durofix' adhesive to the centres of several glass plates. These were exposed to settling barnacles for a few days. They were then taken up and some were wiped thoroughly all over with clean cotton-wool, whilst others were wiped in the same way but leaving the slides barnacled. A pair of these plates was placed side by side, slides uppermost, in each concrete holder, one with the slide barnacled, the other with the slide bare. These pairs were exposed for periods of 2 or 3 days. After each period of exposure the numbers of barnacles on each slide and on the surrounding 199 cm.^{2} of the upper surface of each plate were

TABLE II. SETTLEMENT OF *ELMINIUS MODESTUS* ON PAIRS OF GLASS PLATES

To one plate of each pair a microscope slide bearing a recorded number of barnacles was fixed, to the other a bare slide. Settlement was consistently much heavier on the plate which bore the barnacled slide.

	Plate with barnacled slide				Plate with bare slide		
			Settlement		Settlement		Ratio in favour of plate with barnacled slide
Period of exposure	Initial no. on slide	Final no. on slide	On slide	On plate	On slide	On plate	
6–8. viii	212	287	75	480	Plate lost		—
	249	304	55	599	8	173	3·5 : 1
8–10. viii	287	369	82	354	3	69	5·1 : 1
	304	403	99	540	0	117	4·6 : 1
10–12. viii	369	413	44	66	14	31	2·1 : 1
	403		Plate lost		3	25	—
12–14. viii	14	1	(−13)	23	0	7	3·3 : 1
	413		Plate lost		0	5	—
3–6. ix	160	167	7	141	1	20	6·7 : 1
	85	89	4	116	1	24	4·8 : 1
	410	497	87	230	5	106	2·2 : 1

recorded (see below for details of the counting-frame used), and the plates and one of the slides of each pair were again wiped bare before exposure for a further period. The results are set out in Table II.

Consistently, many more barnacles settled on the plate which bore the initially barnacled slide than on that which bore the initially bare slide. It seems highly probable that these differences were due to gregariousness. They cannot be regarded as due to sheltering, for the recently settled barnacles on the slide were small compared with the thickness of the slide (2 mm.), so that virtually the same degree of shelter was afforded by the bare slide as the barnacled slide. The increment on the barnacled slide was also consistently greater than the number settling on the bare slide, except for one occasion when no barnacles appeared on the bare slide whilst those on the barnacled slide were considerably reduced in number by mortality.

While counting, each plate was placed slide uppermost over graph paper on

which the outline of the slide had been drawn surrounded by ten other concentric rectangles, gradually increasing in area (Fig. 1 c). The plate was orientated so that the slide was superimposed upon its outline on the paper. This outline measured $2{\cdot}6 \times 7{\cdot}5$ cm., the adjoining rectangle $3{\cdot}5 \times 8{\cdot}5$, the next $4{\cdot}5 \times 9{\cdot}5$, and so on. Between the outlines of adjoining rectangles there was therefore a series of areas, gradually increasing in size and distance from the slide, each 0·5 cm. wide. The number of barnacles in each of these areas was recorded and is shown in Table III. The areas are numbered consecutively

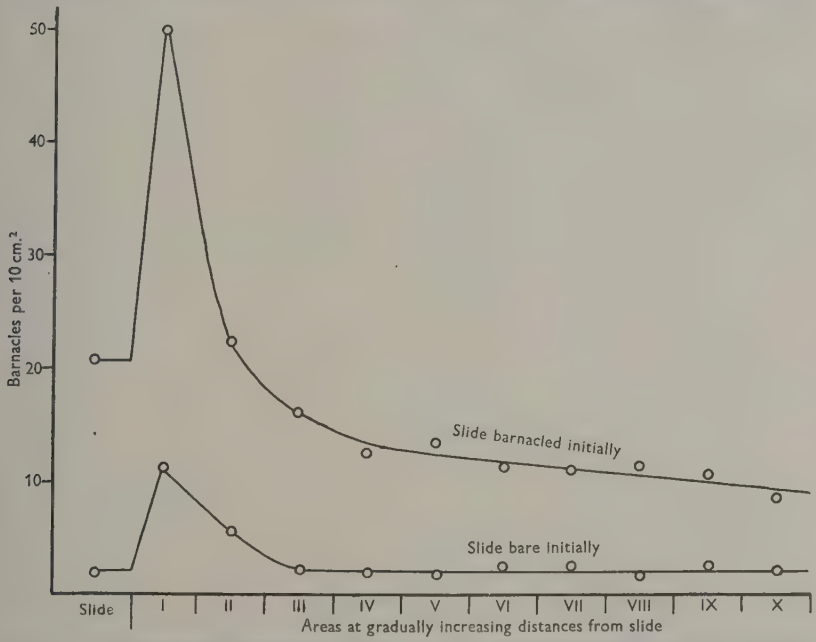

Fig. 2. Mean densities of settlement on slides and on surrounding areas at gradually increasing distances from them (see Fig. 1 c). Data from Table III.

I–X, I being that immediately surrounding the slide. The results relating to the barnacled slides and the bare slides are grouped separately. On the right of Table III the sizes of the areas and the densities of settlement on each are shown. Fig. 2 shows graphically the mean densities of settlement on the slides and at varying distances from them.

Considering first the plates with the slides which were initially bare, it will be seen that while the mean density of settlement on the slides and on the general surfaces of the plates was uniformly low, that on area II was more than twice as great and that on area I five times as great. Evidently the cyprids tended to shelter round the edges of the slides. The densities of settlement on

Table III. Densities of Settlement of *Elminius modestus* on barnacled and bare Microscope Slides and on surrounding Areas of Glass

Areas of glass were marked I–X, each 0·5 cm. wide, I bordering the slide, the remainder at gradually increasing distances from it. Settlement on the initially bare slides and the surrounding glass was uniformly low except immediately adjoining the slide, where increased densities suggest a sheltering tendency. Settlement on and around the barnacled slide was much heavier, gradually decreasing in intensity with increasing distances from the slide. Mean densities are shown graphically in Fig. 2.

	Nos. of barnacles on											Sizes of areas and densities of settlement (nos. of barnacles per 10 cm.^{2})										
Date	Slide	I	II	III	IV	V	VI	VII	VIII	IX	X	Slide	I	II	III	IV	V	VI	VII	VIII	IX	X
												19·8	9·95	13	15	17	19	21	23	25	27	29 cm.^{2}
	Slide barnacled initially																					
6–8. viii	75	41	16	30	46	51	63	45	60	63	65	38·0	41·2	12·3	20·0	27·0	26·8	30·0	19·6	24·0	23·3	22·4
	55	79	67	48	36	49	53	71	79	59	58	27·8	79·4	51·5	32·0	21·2	25·8	25·2	30·8	31·6	21·8	20·0
8–10. viii	82	50	60	45	40	46	23	20	32	24	14	41·4	50·2	46·2	30·0	23·5	24·2	11·0	8·7	12·8	8·9	4·8
	99	131	76	49	28	31	30	52	51	64	28	50·0	131·7	58·5	32·7	16·5	16·3	14·3	22·6	20·4	23·7	9·7
10–12. viii	44	7	1	2	0	0	11	7	0	13	25	22·3	7·0	0·8	1·3	0	0	5·2	3·0	0	4·8	8·6
12–14. viii	0	3	3	2	5	3	1	1	0	3	2	0	3·0	2·3	1·3	2·9	1·6	0·5	0·4	0	1·1	0·7
3–6. ix	7	52	8	8	8	14	11	9	16	12	3	3·5	52·2	6·2	5·3	4·7	7·4	5·2	3·9	6·4	4·4	1·0
	4	40	11	8	12	15	8	5	5	5	7	2·0	40·2	8·5	5·3	7·0	7·9	3·8	2·2	2·0	1·8	2·4
	87	45	23	28	18	21	19	20	14	17	25	4·4	45·3	17·7	18·7	10·6	11·1	9·0	8·7	5·6	6·3	8·6
								Mean densities				20·82	50·02	22·67	16·29	12·60	13·46	11·58	11·10	11·42	10·68	8·69
	Slide bare initially																					
6–8. viii	8	16	17	11	14	9	16	26	16	22	26	4	16·1	13·1	7·3	8·2	4·7	7·6	11·3	6·4	8·1	9·0
8–10. viii	3	5	20	4	1	5	5	10	2	10	7	1·5	5·0	15·4	2·7	0·6	2·6	2·4	4·3	0·8	3·7	2·4
	0	13	7	5	10	6	18	10	9	20	19	0	13·1	5·4	3·3	5·9	3·1	8·6	4·3	3·6	7·4	6·6
10–12. viii	14	8	7	4	1	1	7	1	2	0	0	7·1	8·0	5·4	2·7	0·6	0·5	3·3	0·4	0·8	0	0
	3	1	1	5	3	6	0	3	3	2	1	1·5	1·0	0·8	3·3	1·8	3·2	0	1·3	1·2	0·7	0·3
12–14. viii	0	0	1	0	0	1	4	0	1	0	0	0	0	0·8	0	0	0·5	1·9	0	0·4	0	0
	0	0	0	0	0	0	0	0	2	0	3	0	0	0	0	0	0	0	0	0·8	0	1·0
3–6. ix	1	7	3	0	1	2	0	1	2	4	0	0·5	7·0	2·3	0	0·6	1·1	0	0·4	0·8	1·5	0
	1	12	0	2	0	1	2	0	2	4	1	0·5	12·0	0	1·3	0	0·5	1·0	0	0·8	1·5	0·3
	5	51	16	5	4	5	2	6	4	8	5	2·5	51·3	12·3	3·3	2·4	2·6	1·0	2·6	1·6	3·0	1·7
								Mean densities				1·96	11·35	5·55	2·39	2·01	1·88	2·58	2·46	1·72	2·59	2·13

the slides which were initially barnacled and on the plates which bore them were much greater. Also the mean density on the barnacled slides was twice that on the areas remote from the slides. On area I settlement was particularly intense and on II it was about as intense as on the slide, probably because the gregarious and sheltering tendencies were acting together in these areas. On III and subsequent areas the densities decreased gradually, as the distance from the slide increased. This gradual decrease contrasts strikingly with the uniformly low densities upon the plates with the bare slides. It suggests that gregariousness in *Elminius* is not entirely a habit of settling in small groups, perhaps as a result of contact between crawling cyprids and previously settled barnacles, but that it affects settlement at considerable distances. The results presented in the next section also support this conjecture, which seems plausible to us, since we are inclined to suppose that olfactory perception may be involved (though evidence on this point is lacking). It may be objected that if gregariousness is a response to the diffusion of a water-borne substance the intensity of settlement should vary inversely with the cube of the distance from the group of previously settled barnacles, but it seems unlikely that this relation would hold under the conditions of these experiments, in which the plates were exposed almost continuously to tidal currents of varying intensity.

Comparison between Settlement on Plates exposed in Muddy Areas, where Barnacles were Absent, and in Neighbouring Shelly Areas, where Barnacles were Numerous

As already mentioned (p. 283) settlement of *Elminius* on test-slates used in routine work on oyster production was usually sparse at stations where the bottom was of bare mud. For example, Table IV gives the 1948 records for two such stations and for two other stations where shells (and barnacles) were abundant. The 1949 records showed a similar phenomenon. The length of river covered by these four stations is about 2 miles (Fig. 3), whilst the tidal currents cover over 4 miles on a moderate tide. *Elminius* cyprids were well distributed in plankton samples, so it seems unlikely that inequalities in their distribution could have been responsible for the differences in intensity of settlement in these areas. The slates were held horizontally about 5 cm. clear of the bottom and did not catch much silt. The tidal currents at these stations seemed of similar strength.

Table V records the settlement on sets of glass plates placed on areas of bare mud and areas covered with shell about 50–100 m. apart. The sets on the Shop Laying each consisted of four plates, the others of two plates. They were put down at L.W.O.T., at places where patches of shell lying on the surface of the mud adjoined extensive areas of bare mud. The shores were fairly straight and uniformly sloping, and there were no differences between adjoining areas in respect of exposure to currents or wavelets. At least one of the patches of shell,

that on Potton shore, had been made within recent years by dredgermen dumping ashore *Crepidula* (the American slipper limpet), and it is probable that most of the patches were originally man-made.

TABLE IV. SETTLEMENT OF *ELMINIUS MODESTUS* ON SMOOTH SLATES

Numbers counted on slates (upper/lower surfaces) exposed just below L.W.E.S.T. for weekly periods at four stations near Paglesham, in 1948. Settlement was usually sparser at stations where the bottom was of bare mud.

Period of exposure	Areas of shell		Bare mud	
	Broadrakes	Shop laying	Upper Paglesham Pool	Opposite Potton point
8–17. vi	188/516	714/916	14/8	No record
17–24. vi	404/2705	467/282	210/1016	0/0
24. vi–1. vii	24/64	53/10	7/58	0/0
1–8. vii	47/107	22/44	1/0	0/1
8–15. vii	1/1	26/64	No record	0/0
15–22. vii	9/39	118/136	1/7	77/43
22–29. vii	203/77	1740/899	0/0	308/80
29. vii–5. viii	35/45	1029/349	0/0	96/92
5–12. viii	24/42	3/2	1/0	93/24
12–19. viii	22/15	10/11	0/0	1/2
19–24. viii	2/2	1/1	0/0	13/1
Means	87·2/328·5	380·3/246·7	23·4/108·9	58·8/24·3

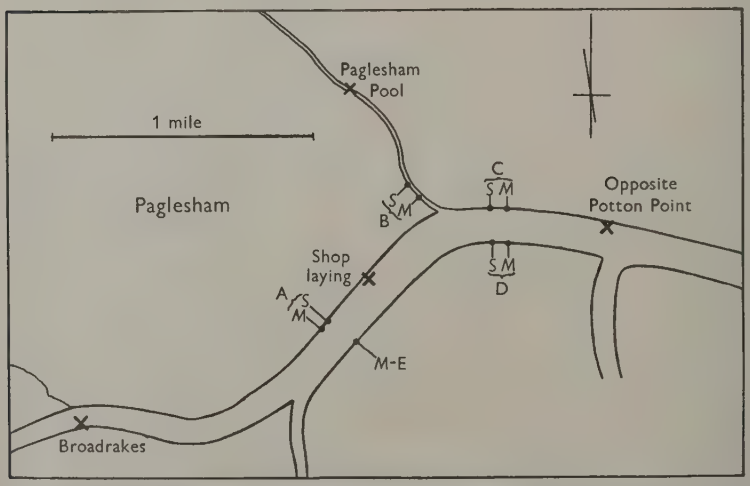

Fig. 3. River Roach near Paglesham at L.W.O.T., showing stations (X) referred to in Table IV. Also, A to D, shore stations referred to in Table V, at each of which plates were exposed on areas of mud (*M*) and shell (*S*); E, muddy area on Potton shore at which plates were exposed for 8 weeks for comparison with plates exposed for the same period on the area of shell at A (p. 294).

Settlement on the plates exposed on the patches of shell was consistently much heavier than on those on adjoining bare mud. The difference was not due

TABLE V. COMPARISON BETWEEN SETTLEMENT OF BARNACLES ON GLASS PLATES EXPOSED AT L.W.O.T., ON NEIGHBOURING AREAS OF SHELL AND MUD

Period of exposure	Nos. on plates placed on an area of shell: Upper surface	Lower surface	Do. area of mud about 50 m. away: Upper surface	Lower surface	Ratio shell/mud: Upper	Lower	Silt on mud plates compared with shell plates
			A. On the Shop laying, Paglesham.				
18–19. vii	470–532–668–511	2–1–5–11	97–2–63*	0–0–0*	10·1 : 1	—	Similar
19–20. vii	470–218–713–260	13–5–6–30	52–41–20–22	2–3–3–0	12·3 : 1	6·9 : 1	Similar
20–21. vii	252–125–231–80	26–5–10–6	0–3–0–0	0–0–4–0	229·3 : 1	11·75 : 1	Slightly more
21–22. vii	451–455–347–291	24–37–10–24	109–79–67*	11–2–9*	4·5 : 1	3·2 : 1	Similar
22–26. vii	6120–5960–6420–3640	610–1196–588–100	726–1620–1140–1640	22–7–6–9	4·3 : 1	56·7 : 1	Similar
26–27. vii	1622–956–1438–1795	121–41–12–11	74–86–140–133	1–0–14–11	13·6 : 1	7·1 : 1	Slightly more
27–28. vii	178–105–646–104	17–39–7–14	0–34–13–7	0–3–1–0	19·1 : 1	19·25 : 1	Similar
			B. In Paglesham Pool.				
19–20. vii	1764–1958	10–8	234–512	14–0	5·0 : 1	1·3 : 1	Similar
20–21. vii	2798–2883	41–74	250–84	2–36	17·0 : 1	3·0 : 1	Slightly more
21–22. vii	2272–3249	162–143	502–755	56–91	4·4 : 1	2·1 : 1	Similar
22–26. vii	6810–7650	1184–972	2660–2560	671–364	2·8 : 1	2·1 : 1	Similar
26–27. vii	1774–826	17–59	234–58	0–20	8·9 : 1	3·8 : 1	Similar
27–28. vii	674–1042	19–7	88–153	1–3	7·1 : 1	6·5 : 1	Similar
			C. On Wallasea Shore, below Paglesham Pool.				
3–4. viii	39–29	1–1	2–4	0–0	11·0 : 1	—	Similar
8–10. viii	325–406	24–2	6–2	2–7	91·4 : 1	2·8 : 1	Slightly more
10–11. viii	85–101	97–12	54–45	34–21	1·9 : 1	2·0 : 1	Similar
			D. On Potton Shore, opposite Paglesham Pool.				
2–4. viii	169–91	0–3	7–11	0–1	14·4 : 1	3·0 : 1	Similar
8–10. viii	421–311	13–41	133–189	10–0	2·3 : 1	5·4 : 1	Similar
10–11. viii	88–120	36–8	30–16	12–20	4·5 : 1	1·4 : 1	Similar

* One plate missing. This was allowed for when calculating ratios.

to varying muddiness of the plates, for there was little difference between the muddiness of the upper surfaces of plates from the two types of ground, whilst the lower surfaces were equally clean. The possibility that it was due to varying turbidity of the water must be considered, for in this respect there were probably frequent slight differences between the muddy and shelly areas. Much of the silt in the water is derived from the muddy bottom, particularly from the shores. It is swirled up by wavelets at low water and, in places, by the current when the tide is running. It would not be surprising to find that settlement is discouraged by turbidity, for such behaviour would be adaptive, leading to avoidance of places liable to smothering by mud, but such behaviour has not yet been demonstrated in *Elminius modestus*. On the contrary, Darwin (1854) remarked on the peculiar ability of this species to live under muddy conditions. Moreover, the plates were held about 5 cm. above the bottom, and the differences in turbidity between adjoining areas were probably small, because the patches of shell were also muddy and were limited in area. It is much more likely that the comparatively heavy settlement on the plates from the areas of shell was principally due to the gregarious tendency, since the small-scale experiments have shown the existence of such a tendency. At each locality there were virtually no barnacles on the bare mud surrounding the one set of plates, but millions, the vast majority *Elminius*, on the shells within a few metres' radius of the other.

A comparison was also made between settlement on sets of plates exposed on muddy and shelly shores for a long period. Areas were chosen on opposite sides of Paglesham Reach, which is a straight stretch of the River Roach. The shelly area was on the shore of the Shop Laying and the other on the almost uniformly muddy Potton shore (Fig. 3). The two sets, each of eight plates, were put out on 12 August 1949. They were visited occasionally. *Ulva* was found to collect round the protecting wire hoops and on the plates themselves, particularly on the Potton shore. This was removed at infrequent intervals. On 7 October 1949 the plates were taken up, having been down for 8 weeks during which settlement was very sparse. The upper surfaces of all plates were covered with almost continuous layers of mud, which were noticeably thicker on the plates from Potton shore. The lower surfaces were clean. Amongst the mud were sparse filaments of *Enteromorpha*, but the only attached animal, besides *Elminius*, was a single specimen of *Balanus improvisus*. The numbers of *Elminius* on these plates (upper/lower surfaces—as usual with glass plates, settlement was much heavier on the upper surfaces) were as follows:

Area of shell (Shop Laying): 1680/88, 1980/55, 1270/213, 1620/500, 1560/111, 970/280, 1360/127, 2140/480.
Bare mud (Potton shore): 3/1, 2/2, 2/0, 0/0, 5/0, 24/0, 1/0, 0/2.

Some of these were recently settled but the majority were large and had probably settled during August.

These great differences could not have been due to the greater muddiness of the Potton shore plates, since the lower surfaces of all plates were equally clean. It is doubtful whether differences in turbidity contributed to them and though it is quite likely that they were partially due to greater blanketing of the Potton shore plates by *Ulva*, they were probably largely due to the gregarious tendency.

Gregariousness as a Factor affecting the Distribution of *Elminius*

Elminius is abundant on the shores of Essex creeks and becomes very crowded on stable substrata, such as pier piles. It is a small, short-lived form which achieves population densities even greater than those of native shore barnacles, since its individuals readily settle one on top of the other. Doubtless its gregarious habit during settlement tends to maintain its littoral distribution.

Away from the shores, at depths of about 5 fathoms for instance, it is comparatively sparse. The majority of shells dredged from these deeper grounds in 1949 bore no *Elminius*, but occasional shells bore many; isolated individuals were rare. In November 1947, *Elminius* was well established, but not common, in the Helford River, Cornwall. On the shore at Calamansack only about one stone in twenty bore any specimens, but some bore groups of from five to twenty. Several isolated individuals were observed in this locality. It was even less common on the oyster-layings in mid-river, where only about one shell in a hundred bore any specimens, yet one shell was observed bearing a group of eight. In the Fal and Truro Rivers few were seen during a week's survey of shores and oyster grounds in June 1949, except at the wharf at Malpas, where the species was abundant.

The tendency to settle in groups and in places where the species is well established must tend to prevent wastage through individuals settling in unsuitable localities and in isolation. It will not prevent the colonization of new areas, for occasional individuals settle in such areas even when settlement is sparse. Groups will gradually form round the majority of these pioneers, so that their breeding capacity will not be wasted and suitable areas will eventually become fully colonized. Far from restricting the spread of *Elminius* in this country, gregariousness will make it more certain, though more gradual. Craft in Essex creeks become heavily fouled with *Elminius* during the summer, and coastal shipping must play an important part in widening its distribution. This fact, together with the gregarious tendency, may partially account for its apparent predilection for wharves, although this is doubtless largely due to intolerance of wave action and insolation.

Summary

A gregarious tendency during settlement, similar to that already demonstrated in oyster larvae, was suspected in *Elminius*, because cyprids settled in groups during the initial stages of colonization of surfaces (crowded later arrivals

showed a spacing-out tendency) and because settlement on test-plates was peculiarly sparse at stations with a muddy bottom, where barnacles were absent.

Settlement was much heavier on areas of smooth glass, which already bore recently settled barnacles, than on similar adjoining areas which were bare.

When barnacled microscope slides were stuck to one set of glass plates, bare slides to another and the two sets exposed side by side, settlement was consistently much heavier on the plates which bore the barnacled slides. The mean density of settlement on the bare slides and the surrounding plates was uniformly low, except for a greater density immediately adjoining the slides, probably due to sheltering alongside their edges. On the barnacled slides density of settlement was much higher and on the plates immediately alongside still more so, whilst at increasing distances from the slides it became gradually smaller but was still much heavier than on the plates with the bare slides. This suggests that the sensory basis for gregariousness can act at a distance. It may possibly be olfactory.

Settlement was very much heavier on glass plates placed on areas of shore where shells were numerous and barnacles abundant, than on similar plates on areas of bare mud 50–100 m. away, where barnacles were absent. This was probably largely because of gregariousness.

In localities where the species was sparse it usually occurred in small groups, loss of breeding potential through isolation being thus at a minimum.

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SOME OBSERVATIONS ON THE EFFECT OF FIBROUS GLASS SURFACES UPON THE SETTLEMENT OF CERTAIN SEDENTARY MARINE ORGANISMS

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(Plate I and Text-fig. 1)

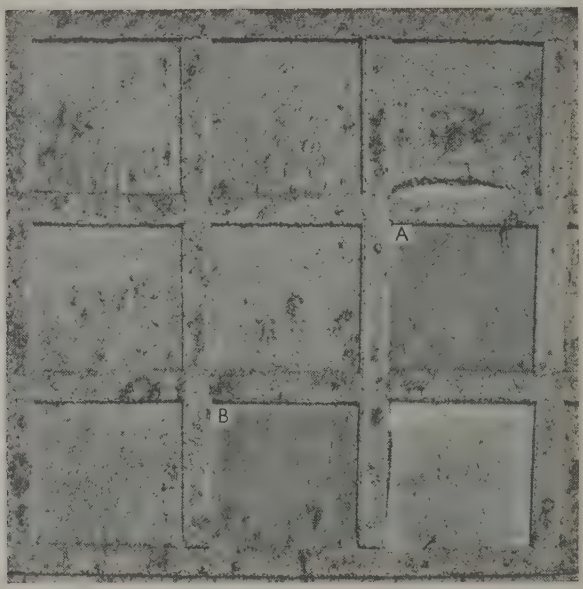
The work of Wilson (1948, q.v. for further references) has emphasized the importance of the nature of the substratum for the settlement and metamorphosis of a number of marine worms, while Pomerat & Weiss (1946) and Pyefinch (1948) have drawn attention to the effect of surface conditions upon the settlement of barnacles. Observations during some recent tests on a number of glass cloths, manufactured by Fibreglass Ltd., have resulted in further evidence concerning the marked effect of surface texture on the settlement of certain sedentary marine organisms.

Samples of these cloths were mounted on both sides of a wooden board and the latter attached to an iron frame which was suspended 2 ft. below the surface from a raft moored close inshore. Duplicate specimens of nine types of cloth were tested, the positions on each side of the board being allocated randomly. Control panels of seasoned Bakelite were exposed at the same time. (No toxic panels were under test on the raft during these exposures.)

The cloths and controls were immersed on 25 March 1949. A barnacle settlement, which subsequently developed into one of the heaviest for many years, began between 1 and 3 April, was heavy by the 5th and continued for some time (Barnes, 1950). At the first inspection (15 April, 21 days' exposure) most of the cloths and the controls were heavily covered with either newly settled cypris larvae or young barnacles.

The exposure was continued and a further examination made on 9 May (45 days' exposure). Four of the samples were almost completely free from barnacles; the remainder and the Bakelite controls were more or less uniformly and very thickly covered with young barnacles, determined later to be *Balanus crenatus* (Text-fig. 1). In marked contrast to this inhibiting effect of four of the Fibreglass panels on the settlement of barnacle larvae, all the panels and the controls were similar with regard to other attached forms, which consisted only of mixed diatom species and some short filaments of *Ectocarpus sandrianus* at the first inspection, with the subsequent addition of traces of *Cladophora* sp. and *Ulothrix flacca*.

The four panels almost free from barnacles were duplicates of two types of cloth and, as a result of inquiries, Fibreglass Ltd. pointed out that these duplicates, while similar to one another, differed from the others in that they were what is termed 'staple' cloths. As such, they are made up of comparatively short lengths of glass fibre spun together to form a strand before weaving into cloth. The other samples, which had not inhibited settlement, were 'continuous' cloths, consisting basically of very long glass filaments. A microscopic examination showed the continuous cloth to have an extremely smooth surface (Pl. I, fig. 1), in marked contrast to the rough spinous surface of



Text-fig. 1. Nine samples of Fibreglass cloth after 45 days' exposure. Note almost complete absence of barnacles on the staple cloths, panels A and B. $\times \frac{3}{20}$.

the staple cloth, resulting from the projecting and partially interlocking free ends of the short, fine glass filaments (diameter 8 μ approx.) comprising the individual strands. The general impression of the surface of these staple cloths was, therefore, of a stiff fibrous weft, beyond which numerous longer fibres (about 1·0 mm. in length) projected (Pl. I, figs. 2, 3).

In view of the strikingly different effect of these two types of cloth upon settlement of barnacles, a second set of panels and controls was put out on 26 July 1949, to ascertain whether there was any similar effect with respect to settling forms prevalent later in the season.

At the first inspection (12 August, 17 days' exposure) only diatoms and traces of algal sporelings were present on all panels and controls. After a further 6 weeks' exposure all had a heavy growth of *Tubularia larynx*, together with some *Laomedea* (*Campanularia*) *flexuosa*, and some panels had a number of newly settled *Pomatoceros triqueter*. At the next inspection (22 October, 88 days' exposure) it was evident that there was a clear distinction with regard to this *Pomatoceros* settlement. The staple cloths that had virtually prevented the settlement of barnacles were quite free from *Pomatoceros* which was, however, present on all the smooth cloths and frequent on some, although no cloth was as heavily covered as the control panels. Continued exposure throughout a further period of heavy *Pomatoceros* settlement, as clearly indicated by the control panels, confirmed the effectiveness of these staple cloths in preventing attachment of this species. The control panels showed that during this period there was a settlement of *Anomia ephippium*, the light character of which settlement makes confirmation of the results necessary, but examination of the cloths suggested that its settlement had been inhibited by the staple yarns.

It appears, therefore, that the texture of the surface of the staple cloth prevents the settlement of *Balanus crenatus* and *Pomatoceros triqueter*, whose larval forms differ widely in both structure and size, but is without effect on the settlement of *Tubularia larynx*.

Visscher (1928) states that cypris larvae, in a series of exploratory movements, may cover appreciable distances before attaching. It is possible, therefore, that during these movements the projecting bristles of the staple cloths by their number and stiff character may prove a source of irritation or may mechanically restrict such exploratory movements, either effect causing the cypris larvae to move away. It is of interest to note that settling oyster larvae are sensitive to the physical texture of the surface, and that they also carry out exploratory movements before settlement and metamorphosis (Prytherch, 1934; Cole & Knight-Jones, 1939). Further, according to these authors, these larvae do move away from an unsuitable surface. It is not clear, however, why such a surface as this staple cloth presents, if actively irritating, does not prevent the settlement of the actinula larva of *Tubularia*, although of course the latter may be less sensitive to this type of mechanical irritation. This larva, according to Pyefinch & Downing (1949), also moves over a surface before settling, but the length of the aboral tentacles would be sufficient to penetrate the fibrous surface weft. A similar explanation has been advanced by these authors to explain the lack of settlement of *Tubularia* on a surface covered by long tufts of filamentous algae, in contrast to its ready settlement on a surface covered by shorter (less than 2 mm. in length) algal tufts. In addition, any irritation of an actinula larva may stimulate discharge of the nematocysts contained within the swollen tips of the attaching aboral tentacles, thus facilitating attachment.

Wilson (1948), working with the larva of the polychaete *Ophelia bicornis*, found that substrata consisting of more angular grains were unfavourable to

settlement and metamorphosis, and he suggested that the size and shape of the interstices between the grains were more important than the grain size or shape, a critical amount of surface area being requisite for the initial attachment stimulus and subsequent metamorphosis. From this point of view the character of the surface of the staple cloth may not provide the appropriate stimulation.

The development of the actinula larva of *Tubularia* is much more direct than the metamorphosis of a barnacle or polychaete larva, and may not require so critical a stimulus for its initiation.

The courtesy of Fibreglass Ltd. throughout these investigations, and in particular the help of their representative, Mr H. Cameron, is acknowledged.

Summary

A description is given of a glass cloth surface which prevents the settlement of larvae of *Balanus crenatus* and *Pomatoceros triqueter*, whilst not affecting that of *Tubularia larynx*. A number of possible causes for this are examined, and its relation to other work on the settlement of sedentary forms is briefly considered.

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EXPLANATION OF PLATE I

Fig. 1. A photomicrograph of surface and folded edge of a smooth continuous cloth. ×60. (N.B. Folding has caused the slight irregularities seen along the edge.)

Fig. 2. The same of folded edge of staple cloth A. The projecting fine glass filaments have diameters of about 8 μ. ×50.

Fig. 3. The same of surface of staple cloth B. ×30.

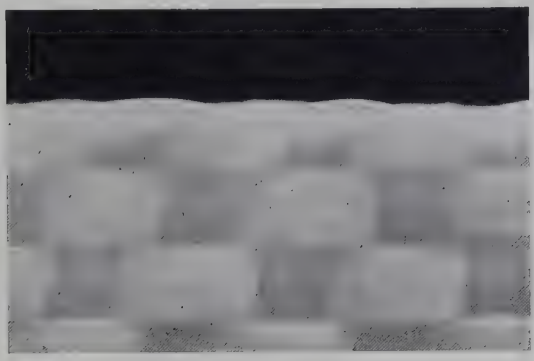

Fig. 1.

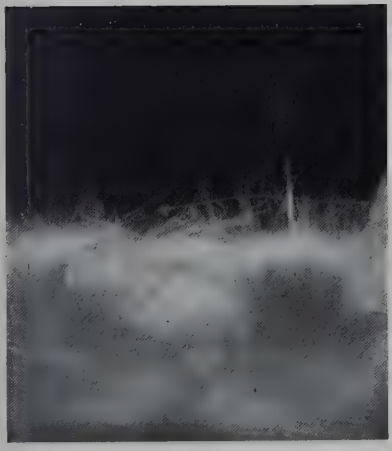

Fig. 2.

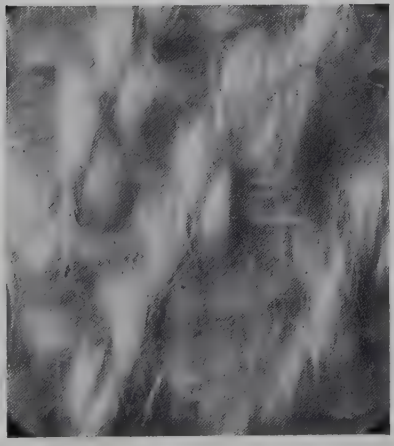

Fig. 3.

RESPONSES OF *BRANCHIOMMA VESICULOSUM* (MONTAGU) TO PHOTIC STIMULATION

By J. A. C. Nicol, D.Phil.

Experimental Zoologist at the Plymouth Laboratory

(Text-figs. 1–6)

CONTENTS

	PAGE
Introduction	303
Methods	305
Observations	306
Photic stimulation and the withdrawal reflex	306
Effect of sudden alteration in intensity	306
Adaptation to photo-stimulation	306
Minimal effective intensity change	307
Sensitivity in lights of different spectral composition	309
Responses of specimens kept in light and darkness	309
Variability in response	311
Differential responsiveness to intensity change and movement	312
Light intensity and emergence from the tube	313
Orientation and movement with reference to light	314
Orientation of tubes to direction of the light (photo-tropism)	315
Discussion	317
Summary	319
References	319

Introduction

The light sensitivity of sabellid and serpulid polychaetes has been investigated on a number of occasions, but this subject is still poorly understood. Early workers commented on the extreme sensitivity of certain species to various stimuli, including changes in illumination. These animals are tubicolous, and normally they protrude their branchial crowns from the mouths of their tubes. When disturbed the animal usually jerks back into its tube. This quick withdrawal is the result of synergistic contraction of the longitudinal muscles, and it is intermediated through a giant axon system (review by Nicol, 1948*a*).

Many, perhaps all, species of the Serpulimorpha retreat into their tubes on interruption of the light or during the passage of shadows. This response is reported for: *Sabella spallanzanii* (Viviani), *S. microphthalma* Verrill, *Bispira volutacornis* (Montagu), *Potamilla reniformis* (O. F. Müller), *Branchiomma vesiculosum* (Montagu), *B. vigilans* Claparède, *Dasychone bombyx* (Dalyell), *Myxicola infundibulum* (Montagu), *Eudistylia polymorpha* (Johnson), *Hydroides dianthus* (Verrill), *H. uncinata* (Philippi), *Serpula vermicularis* L., *Pomatoceros*

triqueter L., *Protula intestinum* (Lamarck) (Dalyell, 1858; Gosse, 1863, 1877; Claparède, 1868, 1870; Soulier, 1891; Andrews, 1891; Hesse, 1899; Hargitt, 1906, 1909*a*, *b*, 1912; Buddenbrock, 1913, 1928; Hess, 1914; Loeb, 1918; Ricketts & Calvin, 1939; Nicol, 1948*b*; *et al.*). Observers have noted that animals react to sudden decreases in light intensity, to moving shadows, and to slight movements of the observer within view of the animal. These are largely qualitative impressions. A response certainly occurs to a sudden decrease, but not to a sudden increase, in light intensity, for example in *Hydroides dianthus* (Hargitt, 1906) and *Serpula vermicularis* (Hess, 1914).

Evidence from ocular structure is ambiguous. *Branchiomma vesiculosum*, which possesses ocular spots near the tips of its branchial filaments, withdraws into its tube when the light dims; it still gives this response when the ocular spots are removed (Hesse, 1899). In *Hydroides dianthus*, which possesses no such special branchial receptors, the withdrawal reflex is equally well developed. Photo-sensitivity is greatest in the distal quarter of the filaments; total ablation of the filaments abolishes the reflex (Andrews, 1891; Hargitt, 1906). Consequently, it would appear that the specialized ocular organs on the branchial filaments are not necessary for this response (cf. Hesse, 1899).

Constant illumination also acts as a stimulus for other behavioural activities in some of these sedentary polychaetes. Loeb (1906, 1918) claimed that *Sabella spallanzanii* and *Hydroides uncinata* turn their branchial crowns and the anterior portion of their tubes towards the source of the light. This behaviour would constitute a kind of photo-tropism. Hargitt (1909*a*, *b*, 1912), who repeated Loeb's experiments, found no evidence for orientation towards the light, but Fox (1938) considered that *Sabella spallanzanii* is positively phototropic. No conclusion seems possible without reinvestigating the subject.

Again, Fox (1938) found that *S. spallanzanii* is usually retracted within its tube during the day, and emerges at night; other observers also indicate that *S. pavonina* protrudes its crown mainly at night. This is a negative postural response to light intensity.

The following account presents the results of experiments carried out on photo-sensitivity in the sabellid worm, *Branchiomma vesiculosum*. This species was chosen because it is available in quantity, it is large, hardy in the laboratory, and because it displays a well-marked light reflex when compared with *Sabella* and *Myxicola*, the two other large species which are common locally. The photo-receptors and the physiological mechanisms involved will be described in a further paper.

Dr W. R. G. Atkins, F.R.S., and Mr F. J. Warren have provided technical assistance and advice, particularly in the measurement of illumination. I am especially grateful for their calibration of incandescent lamps, a photoelectric cell, and galvanometers. Dr Atkins and Mr F. S. Russell F.R.S., have read the manuscript. I thank them for their advice and criticism.

Methods

Animals were kept in dishes under circulation in the laboratory, and specimens were chosen at random for any particular experiment. The experiments were carried out in a cellar where the temperature remained fairly constant for long periods; the seasonal variation over 6 months was 6° C.

Intensity measurements were made with a selenium rectifier photocell ('Electrocell', German make) which was calibrated for absolute photosensitivity against a substandard lamp. The sensitivity of this cell ceased to be linear above 25μA., with a high resistance galvanometer, and a correction was applied to readings at higher intensities. Readings were made on a Gambrell Bros. Onwood patent galvanometer (557·3Ω at 17·75° C.) and on a Cambridge unipivot galvanometer (9.99Ω at 17·75° C.). These were calibrated in terms of each other and against a potentiometer and accurate resistances. Their sensitivities, respectively, were 0·27 and 1·92 μA. per scale division, and they were read to a 0·2 scale division. Reduction of intensity was achieved on occasion by the use of a Chance ON 31 neutral filter 3·5 mm. in thickness. This filter, according to the manufacturer, gives nearly uniform transmission from 4000 to 7000 A. Its overall transmission measured in the visible spectrum was 8·2 %.

For obtaining light from restricted spectral regions, a set of four Corning coloured filters was used. These same filters have been described and their characteristics presented by Atkins & Poole (1931). These were: C. dark blue (H. lantern blue) with 20 % transmission of visible light, 50 % cut-off at 4800 A., and very slight transmission in the red; C. sextant green, with a transmission of 2·2 % of visible light, and 50 % cut-offs at 5000 and 5700 A.; C.H.R. yellow, green shade, with 50 % cut-off at 5500 A., and 67 % transmission of visible light; C. selenium red G. 24, with 50 % cut-off at 6400 A., and 66 % transmission of visible light.

Unless otherwise specified, the following additional experimental conditions obtained. The light source was a 100 W., gas-filled tungsten 'daylight' lamp (Crompton), maintained at 200 V. by a variable transformer (Variac). The animals, in their tubes, were placed in an aquarium with a glass front. The transmission of this glass, measured with the selenium rectifier photocell and coloured filters specified above, was: 88·7 % in unfiltered ('white' light); 88·3 % in blue light; 89·7 % in green light; 88·9 % in orange light; 83 % in red light. These figures were used to correct the intensity measurements made in front of the aquarium glass. No allowance was made for absorption by sea water; the animals lay 1–5 cm. behind the glass; usually some part of the crown was within 2 cm. of the glass. The inside of the tank was dark brown; a piece of matt-black paper covered the rear wall. At very low intensities, when it was difficult for the partially dark-adapted eye to distinguish the animals, a piece of white paper was placed at the back of the tank. Under these conditions, reflectance was not measurable with the photocell. The arena in front of the

tank contained a movable lamp housing; this area was enclosed and was painted matt-black.

Branchiomma is extremely sensitive to mechanical stimuli, and reacts promptly to vibrations of low intensity. The aquarium was mounted on a brick column topped with a slate slab, and the column rested on a concrete floor founded on solid rock. Even with this rigid arrangement, and with two inches of felt between the slate and the bottom of the aquarium, it was not possible to damp all vibrations to below the threshold of sensitivity of the animals.

Observations

Photic stimulation and the withdrawal reflex

Effect of sudden alteration in intensity

Specimens of *Branchiomma vesiculosum* frequently withdraw into their tubes when the light is suddenly extinguished. In several thousand trials no specimen ever withdrew in response to sudden increase in intensity of illumination. Response to intensity change, therefore, is to decrease, not increase, in intensity. This agrees with results obtained for *Hydroides dianthus* and *Serpula vermicularis* (Hargitt, 1906; Hess, 1914; cf. also Buddenbrock, 1928).

Adaptation to photo-stimulation

When the light is suddenly diminished, the animals respond to the first stimulation or first few photic stimuli by a withdrawal, but thereafter cease to react. In Fig. 1 are shown the results of subjecting the worms to repeated

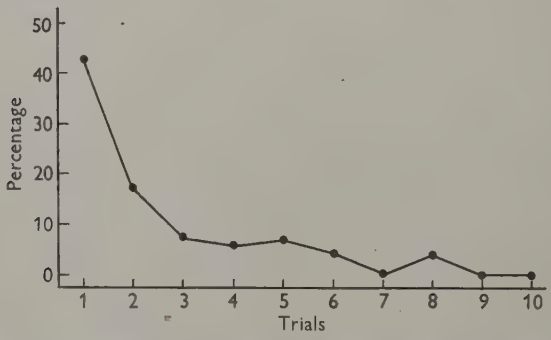

Fig. 1. Course of adaptation to photic stimulation (sudden decrease in intensity). Ordinates, proportion of animals responding; abscissae, successive trials.

stimulation. The animals were placed in white bowls underneath a white (pearl) tungsten lamp (100 W., 200–230 V. input). The measured intensity at the level of the containers was about 419 lux. Successive stimuli were delivered

usually at intervals of 1–10 min. It was not possible to standardize the interval because of great variability in times of emergence in different animals. About half the animals responded to the first stimulus; thereafter the number responding rapidly decreased to zero at the ninth trial. Adaptation or habituation to photic stimulation has been reported for other Serpulimorpha, namely, *Hydroides dianthus*, *Serpula vermicularis* and *Bispira volutacornis* (Bohn, 1902; Hargitt, 1906; Hess, 1914).

Minimal effective intensity change

The limen for decrease in light intensity at different initial intensities was determined as follows. Two daylight lamps were used at empirically dermined distances so as to give a certain initial intensity and a certain decrease in

Table I. Limen for Decrease in Photic Intensity at Eight Different Initial Intensities

Further explanation in text.

Initial intensity i (lux)	Lowest effective decrease in intensity tested δi_e (lux)	Highest ineffective decrease in intensity tested δi_i (lux)	$\delta i_e/i$	$\delta i_i/i$
407·2	17·2	12·9	0·0423	0·0317
308·1	12·9	8·6	0·0406	0·0279
185·3	12·9	8·6	0·0698	0·0465
64·6	4·3	2·2	0·0666	0·0334
34·7	2·9	2·2	0·0870	0·0620
17·9	2·9	2·5	0·1600	0·1400
5·3	1·2	1·1	0·2300	0·2030
2·3	0·5	0·4	0·2240	0·1550

intensity when one lamp was extinguished. At each initial intensity animals were tested to determine the minimal intensity change necessary to evoke a response, and the maximal intensity change that failed to evoke a response. All samples used in these tests were drawn from one laboratory group.

The results have been plotted in Fig. 2 as $\delta i/i$, where δi is the minimal intensity change that evoked a response. The vertical lines represent the interval between this effective value and the maximal non-effective intensity change that was determined. Absolute values are presented in Table I. The procedure was very slow and tedious, and to obtain these figures many more observations were required than those shown and utilized. The variability of this biological material will be discussed in a later section. Here it is noted that these results are not interpreted as representing the absolute photosensitivity limits of this species under manifold conditions. The stimulus-response method as here employed does give an indication of what these animals can do under these particular conditions but not necessarily of their ultimate discriminatory powers. These observations were all obtained on a given lot of worms in which all animals were kept under similar conditions,

and were tested in one period of time. It is therefore submitted that the observations are of value as relative and comparative data.

The curve in Fig. 2 shows that a relatively greater intensity change is required to effect a response at low intensities than at high intensities over the range explored (2·32–407·19 lux.).

These results obviously do not conform to the Fechner-Weber law for intensity discrimination. Comparable results are not available for other polychaete species. Hess (1914) sought the minimal decrease in intensity that would evoke a response in *Serpula vermicularis*. He found that moving a lamp from 60 to 61·5 cm. called forth retraction of the crown. The relevant

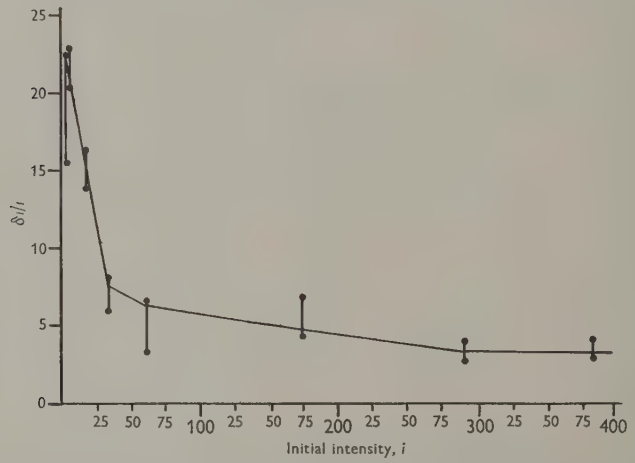

Fig. 2. Relation of minimal decrease in intensity necessary to evoke a response to initial intensity. Ordinates, $\delta i/i \times 100$; abscissae, intensity i, in lux. The data are grouped in pairs for a given value of i. The upper point of each pair represents the minimal value at which a response occurred; the lower point the maximal value at which no response occurred; vertical lines represent the unexplored range. Each point is based on trials of at least 10 specimens.

intensities were as 1:0·95; this gives a value for $\delta i/i$ of 0·05. This is within the range determined for *Branchiomma*. Hecht (1924) has studied an analogous situation in *Mya arenaria*. He utilized retraction of the siphons as an indicator of discrimination, and he tested for sensitivity to increases in light intensity. Hecht also found that the ratio $\delta i/i$ is not constant for this species at different initial intensities; the ratio decreases as intensity is increased up to a certain point, beyond which the ratio increases. However, the Fechner-Weber law for visual discrimination does not hold even in man, the subject for which it was erected. 'For visual intensity discrimination $\Delta I/I$ is approximately constant over the range from medium to very high light intensities, and below these

increases very markedly' (Rawdon-Smith, 1938, p. 18). Since *Mya* is responding to an increase in intensity, and *Branchiomma* to a decrease, it is suggested that the underlying photochemical reactions are similar, but that differences exist in the nature of the central correlatory mechanisms.

Sensitivity in lights of different spectral composition

The following experiments were designed to obtain information for sensitivity to lights of different spectral composition. The lowest initial intensities of light at which a response could be obtained by reduction of intensity were sought. Animals were tested in white and coloured lights of different initial intensities by cutting off the light (reduction to zero intensity). 'White' light from a daylight bulb, blue, green, orange and red lights were used (spectral composition described above under methods). Experiments were carried out on a single sample of worms kept under similar conditions.

White light. The minimal light intensity at which a response occurred to complete extinction of illumination was 2·5 lux. Only one animal in ten contracted at this intensity. At higher initial intensities a greater proportion of animals responded amounting to 80 % at 175 lux (Fig. 3).

Coloured lights. The minimal intensities at which a response could be elicited, and the maximal intensities at which no response occurred to diminution of intensity were determined for blue, green, yellow and red light. The coloured filters used have been described above under methods. The values obtained were weighted for the spectral composition of light from the source, and the spectral sensitivity of the photocell. The results are presented in relative units as the reciprocals of the intensities determined. This gives some indication of relative sensitivity to different spectral regions. The values obtained are green 6–18, blue 3–8, yellow 7–10, red 1·6–2·4 (units of relative sensitivity). The wide spread between the values in green and in blue light is due to the fact that the photoelectric cell has maximal sensitivity in green light (5700 A.) and sensitivity falls off much more rapidly in long than in short wave-lengths (Lange, 1940). The difference between the two figures for green light actually represented only 0·1 μA. in photoelectric current.

The data show that *Branchiomma* is sensitive to the whole visual spectrum from 4000–7000 A. Owing to the spread of the data it is not possible to make a firm statement for relative sensitivities in different spectral regions. Sensitivity is least in the red, increases for shorter wave-lengths, and probably has a maximum between 5000–6000 A. These conclusions require confirmation.

Responses of specimens kept in light and darkness

The effect of retention in total darkness on the withdrawal response of *Branchiomma* was investigated as follows. Specimens were kept in an aerated container in the dark for 5 and 10 days. Sensitivity in weak illumination was thereafter determined by permitting the animals to expand at some given

intensity, and then turning off the light. As a control, an equal number of specimens was kept in constant illumination (257·5 lux) for 5 and 10 days.

Specimens retained in darkness:
(i) For 5 days. Tested at 1·97 lux. Proportion of animals responding: 60 %.
(ii) For 10 days. Tested at 0·36 lux. Proportion of animals responding: 70 %.

Specimens retained in constant illumination (257 lux):
(i) For 5–8 days. Tested at 0·72 lux. Proportion of animals responding: 30 %.
(ii) For 9–10 days. Tested at 0·36 lux. Proportion of animals responding: 27 %.

The data show that animals kept for periods up to 10 days in either constant light or darkness are sensitive to light of intensity at least as low as 0·36 lux. It is probable that the animals are sensitive to weaker intensities, but 0·36 lux was about the lowest intensity at which it was possible to observe the animals. There is slight evidence for greater responsiveness of animals maintained in darkness than in light, but not for greater sensitivity to weak light. Owing to voltage variation in the power mains the light occasionally flickered. Illumination of specimens kept in the light was therefore constant, but light intensity occasionally dropped momentarily. These sudden decreases in light intensity were sufficient to cause the animals to react. If these results are compared with the figure for minimal intensity of white light given on p. 309 it will be seen that the minimal intensity at which the animals responded is only one-seventh as great in the present experiments. Corresponding observations on other tubicolous polychaetes are conflicting. Hargitt (1905) found that in *Hydroides dianthus* specimens obtained from deep water (20 fathoms), or kept in a dimly lighted basement over winter, failed to respond to shadows. Bohn (1902), however, noted that in *Hermella ascolata* prolonged exposure to sunlight tended to weaken the sensitivity of the worm to reduction in photic intensity. He explained the reaction to shadows as a learnt response, based on mechanical factors as the unconditioned stimuli. Copeland (1930) has demonstrated the possibility of establishing a conditioned response in a specimen of *Neanthes virens* by associating feeding with light diminution and increase. Yerkes (1906) selected two specimens of *Hydroides dianthus* that failed to respond to shadows, and she repeatedly subjected them to reduction of photic intensity, followed by weak tactile stimuli. After a training period the animals became conditioned to react negatively to shadows.

Interspecific variation may explain some of the differences listed above. But apart from this factor it is clear that the previous history of the animal has considerable influence upon its responsiveness to decrease in light intensity, and upon the threshold of light intensity at which a response can be elicited. The operating factor in *Branchiomma* seems to be not the level of light intensity to which it was generally exposed, but the frequency or infrequency of stimulating decreases in intensity. When animals are kept for some time in either light or darkness and are undisturbed, more react to decrease in light

intensity, and at much lower initial intensities, than when kept under other laboratory conditions where they are frequently subject to variations in light intensity. Repetitive photo-stimulation leads to a lasting state of apparent habituation in which the energy change required to evoke a response is also raised.

Variability in response

It has already been intimated that different animals show considerable variability in their response to photic stimulation. For this reason, when determining critical values, a sample of at least ten specimens was tested (occasionally increased to eleven or twelve specimens). In Fig. 1, which illustrates the course of adaptation to repeated photic stimulation, two aspects of variability are depicted. This graph is based on examination of fifty-six specimens, of which only twenty-four (43 %) responded to the first photic stimulation (intensity 419·13 lux, p. 306). Considerable variation thus exists in the responsiveness of different animals within a population to intensity diminution as a stimulus-signal. The second aspect lies in different rates of adaptation in different animals, some ceasing to respond after the first stimulus, others continuing to respond for nine or more stimuli. Fig. 3 shows still another aspect of individual variation, namely, differences in the number of animals that respond to diminution of illumination at different intensities. In these experiments samples of ten animals were tested at different initial intensities by turning off the lamp. The observations form a fairly regular series from the lowest intensity tested, 2·51 lux, at which 10 % of the animals responded, to 174·6 lux, at which 80 % of the animals responded. In the previous section it has been noted that animals kept under conditions of minimal disturbance have greatly enhanced sensitivity at low intensities. Presumably the behaviour of these animals approaches that of animals living under natural conditions.

Individual differences in the responses of different worms to light have been noted by Andrews (1891) and Hargitt (1906) for *Potamilla* and *Hydroides*. In practice one would expect to find a normal variability in behaviour such as one encounters in investigating any species of animal. The data for *Branchiomma*, however, also suggest a process of adaptation akin to learning, which can modify the withdrawal reflex. Adaptation leads to cessation of the withdrawal response on repeated stimulation, and it raises the limen for photic stimulation.

Following withdrawal there is great variation in the time taken to re-emerge in different animals. The length of time during which the animals remained within their tubes following repetitive photic stimulation was recorded for 35 specimens. In the first three trials, the average periods of withdrawal were 3·9, 3·8, 3·9 min. The means of the differences between the periods of withdrawal in the first and second, and second and third trials, were 0·19 and −0·06 min. respectively. Thereafter, as the number of observations greatly

declined, the mean figures became very variable, without any apparent trend. The observations from the first three trials would indicate that, on the average, animals tend to remain the same length of time in their tubes before expanding their branchial crowns again.

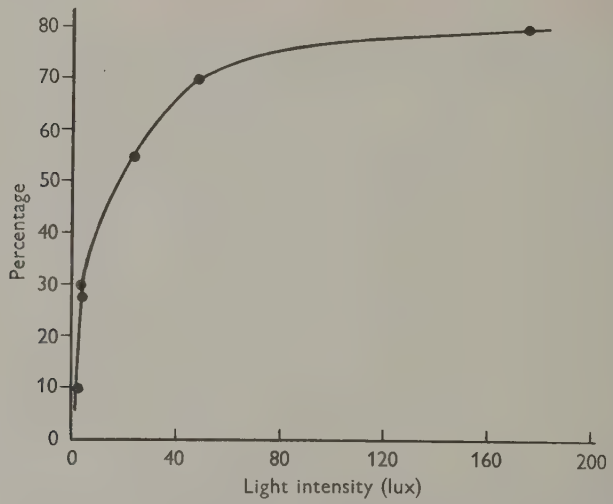

Fig. 3. Proportion of animals that respond to decrease in illumination at several initial light intensities. Ordinates, proportions of animals responding at selected initial intensities; abscissae, light intensities in lux.

Differential responsiveness to intensity change and movement

Two lots of animals were repeatedly stimulated by turning off the light for ten successive trials. Immediately following the last (tenth) trial with this stimulus, a black card was moved across the field between the lamp and the animal for another ten trials. The source of light was a white (pearl) 100 W. tungsten lamp. The intensity at the level of the animals was 419 lux. When the lamp was turned off, the intensity fell to zero. When the card was removed in front of the lamp the intensity fell to about 29 lux. The results are depicted graphically in Fig. 4.

The results show that after the animals have become adapted to a sudden decrease in intensity, they are still sensitive to a moving shadow or moving intensity change of nearly the same magnitude. Slightly less than half the animals responded to a sudden decrease in intensity and to a moving shadow (38·1 and 42·9 % respectively). There is a distinct difference, on the other hand, in the course of adaptation which takes place more slowly to a moving shadow, than to sudden decrease in light intensity. To both events the response

is the same, and the effective stimuli involve diminution in photic intensity, slightly less in movement of the card than in sudden extinction of the illumination. The different adaptation curves show that two distinct sensory processes are involved. This difference arises ultimately from the fact that the one stimulus (the moving shadow) includes a varying temporal and spatial component, as well as an intensity change. Further experiments to elucidate the processes and the photo-receptors involved will be described in a later paper.

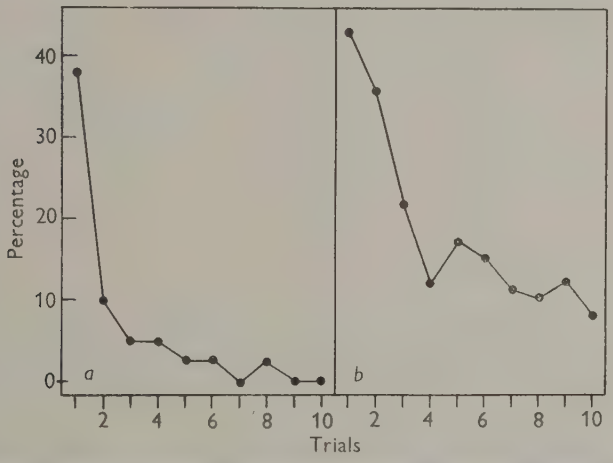

Fig. 4. Course of adaptation to photic stimulation: (*a*) sudden decrease in intensity; (*b*) moving shadow. Observations of 42 specimens. Initial intensity 419 lux. Ordinates, proportions of animals responding; abscissae, successive trials. Trial *b* 1 followed immediately after *a* 10.

Light intensity and emergence from the tube

The following experiments were designed to seek whether the intensity of illumination governs protrusion of the branchial crown from the mouth of the tube. It was not practicable to secure the necessary observations from animals in their natural habitat; consequently, laboratory study had to suffice. Animals were chosen that had recently been collected from their natural habitat, and they were tested within 48 hr. of reaching the laboratory. Twenty-three animals were used. These were placed in the aquarium, which was successively illuminated at four different intensities. Each lot of animals was kept under observation for 30 min.; time of emergence and number of animals that emerged were recorded for each group. The data obtained are presented in Table II. The intensities used were 13·93, 20·04, 125·22, and 689·56 lux. The mean proportion of animals that emerged at all intensities in 30 min. was 80·4 %, and the average time to emerge at all intensities was 10·05 min. There is no apparent trend in the numbers of animals that emerged at different

intensities. The mean times of emergence might be taken to indicate that the animals tend to protrude their branchial crowns sooner in strong than in weak light. However, the length of time which different animals spend in their tubes is very variable; on this basis a difference of 5·3 min. is not significant. In any event, there is no evidence, from these observations, that *B. vesiculosum* is principally a nocturnal form and that it tends to withdraw or remain in its tube when illuminated, as does *Sabella* (cf. Fox, 1938).

Table II. Emergence of Worms from their Tubes in Light of different Intensities

The number of animals tested at each intensity varied from 19 to 23.

Light intensity (lux)	Proportion of animals emerging (%)	Mean time to emerge (total time of observation, 30 min.) (min.)
13·9	76·2	12·5
20·0	84·6	10·3
125·2	73·9	10·2
689·6	86·9	7·2
Mean at all intensities:	80·4	10·05

Orientation and movement with reference to light

Branchiomma vesiculosum is one of those sabellids that can burrow, build a new tube, and survive when deprived of its former tube. On occasion it abandons its old tube spontaneously (Soulier, 1891; Buddenbrock, 1913). Animals removed from their tubes and placed on sand immediately commence to burrow; they are positively geotropic (Buddenbrock, 1913). When placed on a hard surface, such as a glass dish in which burrowing is impossible, they

Table III. Oriented Locomotion away from the Light

Time (hr.)	No. of animals in Light	No. of animals in Shade	Proportion of animals in shade (%)
1417 (start)	6	5	45·5
1517	3	8	72·7
1618	1·5	9·5	86·4
1715	0	11	100·0

usually glide along backwards by slow undulatory waves. Since the animals are capable of free locomotory movement, it is necessary to consider whether light acts as a token stimulus by which they can orientate themselves.

To test orientation to light, groups of 10–11 animals were placed in a white enamel pan, 24 × 33 cm., with overhead illumination. The light source was a white (pearl) tungsten lamp. One half of the dish was covered by a black card. The intensity in the illuminated half of the dish was about 145 lux. A protocol of an experiment is given in Table III, and the data are plotted in Fig. 5.

In these experiments all the animals moved into the shaded half of the container in 4 hr. Consequently, they display negative orientation to light. Orientation under these conditions could be to an intensity difference, or to direction of the light (lateral reflectance from the walls of the dish; cf. Ullyott, 1936). Further experiments are in progress to determine the mechanism of orientation in this species.

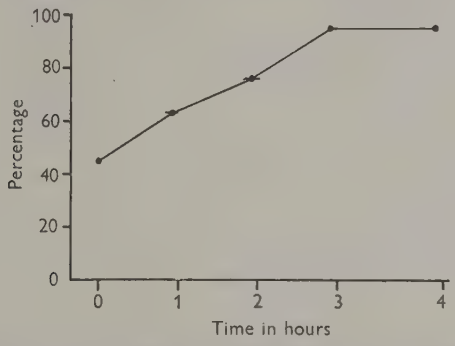

Fig. 5. Oriented movements away from light into shaded region. Ordinates, proportion of animals in shaded portion of container; abscissae, time in hours. Data obtained from two experiments and twenty-two animals. One animal apparently was injured; this would account for the leveling off of the curve slightly below 100 %. Further explanation in the text.

Orientation of tubes to direction of the light (photo-tropism)

The possible influence of the direction of incident illumination on the orientation of the animals' tubes was investigated as follows. Specimens were removed from their tubes, and placed on the surface of clean sand in the bottom of an aerated aquarium. Black matt paper was used to cut off unwanted illumination. Diffuse light was obtained from a 100 W. white (pearl) tungsten lamp. Animals were subjected to total darkness, and to lateral illumination.

About twenty specimens were placed in the aquarium for each test. Most of the animals immediately started to burrow downwards into the sand. A few animals failed to burrow and these were discarded after 2–3 days. The remaining animals were examined. The general direction in which the branchial crowns pointed was noted, and two measurements were made for the protruding section of each tube, namely, the angular deviation from the vertical towards either side of the aquarium, and towards the front or rear of the aquarium. The data obtained are shown below and in Fig. 6.

Specimens building new tubes and subject to horizontal illumination (from front of aquarium). Two days.

(1) No. of specimens—19 (two failed to burrow). Fourteen specimens directed their crowns towards the light. Four specimens directed their crown laterally and towards the light.

Angular deviation from the vertical towards the sides of the aquarium:

Aggregate 190° right, 190° left. Mean 0°

Angular deviation from the vertical towards the front and rear of the aquarium:

Aggregate 630° front, 0° rear. Mean 37° front

(2) Specimens building new tubes in total darkness. 3 days. No. of specimens—19 (1 failed to burrow). Branchial crowns pointed randomly in all directions.

Angular deviation from the vertical towards the side of the aquarium:

Aggregate 200° right, 140° left. Mean 3·3° right

Angular deviation from the vertical towards front and rear of the aquarium:

Aggregate 120° front, 295° rear. Mean 9·7° rear

(3) Specimens subject to horizontal illumination for five days after previous sojourn in darkness (same specimens as in (2) above). No. of specimens—17. Eleven specimens directed their crowns towards the light (front of aquarium). Four specimens directed their crowns to rear of aquarium. One specimen directed its crown to one side.

Angular deviation from the vertical towards the side of the aquarium:

Aggregate 80° right, 230° left. Mean 8·3° left

Angular deviation from the vertical towards the front and rear of the aquarium:

Aggregate 460° front, 90° rear. Mean 22° front

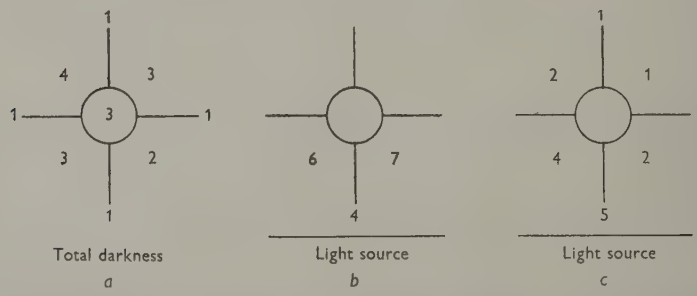

Fig. 6. Diagrammatic representation of the effect of light on direction in which tubes point. The figure in the central circle represents the numbers of animals that directed their tubes and branchial crowns vertically upwards. The figures opposite each radius represent the numbers that directed their crowns and tubes towards the left, right, front or rear of the aquarium. The figures in each quadrant represent the numbers of animals that inclined their tubes and crowns in that direction. It is to be noted that rarely is a tube bent so that it is parallel to the ground; the mean angular deviation from the vertical is given above. A horizontal line beneath the diagram represents the relative position of the light source. (*a*) Total darkness for 3 days. (*b*) Horizontal unilateral illumination for 2 days. (*c*) Horizontal unilateral illumination for 5 days after previously being in the dark for 3 days.

There is definite evidence from these experiments that *Branchiomma* directs the distal portion of its tube and, in consequence, its branchial crown towards the light. Specimens kept for 3 days in total darkness built new tubes which inclined randomly in all directions, but predominantly upwards (Fig. 6*a*). Specimens kept for 2 days in an aquarium illuminated from one side built

new tubes, all of which inclined towards the light. The mean deviation from the vertical towards the light source (90° to the vertical) was 37° (Fig. 6*b*). Finally, specimens which had been in the dark for 3 days, were subjected to unilateral illumination for 5 days. At the end of this period 69 % of the specimens were pointing towards the light, and the mean deviation from the vertical towards the light source was 22°, an increase of 37 % and 31·7° for unilateral deviation over corresponding values for previous sojourn in darkness (Fig. 6*c*). It is concluded that *Branchiomma* tends to direct the exposed extremity of its tube towards the light when building a new tube, and can alter the direction in which the tube points, to conform to a change in the direction of incident illumination.

Discussion

There is no lack of explanation for the value of the withdrawal reflex to tubicolous polychaetes. Jenkins (1940, p. 479) summarizes the prevalent concept when he says: 'It is a common observation that various species of flatworms, annelids and nematodes respond in characteristic fashion to sudden changes of intensity....For instance, the tubicolous annelids, such as *Hermella ascolata* [Sabellariidae] usually retract the tentacles into their tubes with the onset of shadows. This is probably a type of anticipatory response, as if to shadows cast by carnivorous swimming animals.' (cf. Buddenbrock, 1928, p. 12). Known enemies of tubicolous polychaetes are certain species of flatfish, notably the lemon dab (*Pleuronectes microcephalus*) and the sole (*Solea vulgaris*) (Steven, 1930; Wilson, 1935). The evidence is presumptive that they would feed upon *Branchiomma vesiculosum* when available. All stimuli to which *Branchiomma* responds by a withdrawal reflex, namely touch, mechanical vibrations, and decrease in photic intensity, could be token signals of the approach of a predator. In this regard the animal's sensitivity to a moving shadow or intensity change is of particular interest. To a sudden decrease in intensity the animal soon adapts itself, but adaptation to a moving shadow, in general, is considerably slower. Predation involves movement, and it is of advantage to the animal to maintain considerable sensitivity to a token stimulus of a predator's approach. On the other hand, tidal movements and currents in the lower littoral and sublittoral zone can create conditions in which there are regular and repetitive changes of light intensity and, accordingly, photic stimuli without biological significance to the animal. Presumably, adaptation represents a compromise between two conflicting needs of the organism, withdrawal to escape from enemies, and maintained expansion for feeding and respiration. Adaptation also occurs to certain qualities of mechanical stimuli, namely water currents and vibrations; the proportion of animals that respond is greater, and the course of adaptation is slower, than to photic stimulation. Adaptation, apparently, does not occur to tactile stimuli (above the levels of muscular and nervous fatigue). These mechanical

stimuli have greater biological significance and urgency to the animal, in terms of survival value.

For the animal, normally living in its tube, the steady or slowly varying intensity of illumination is apparently without significance in daily behaviour. *Branchiomma* expands its branchial crown in light or darkness in contrast to *Sabella* which is nocturnal (Fox, 1938). This may explain why the light reflex is more highly developed in *Branchiomma* than in *Sabella*, two closely related species living side by side in practically the same niche. The light reflex has greater biological value to *Branchiomma*, which feeds in the daytime, than to *Sabella*, which tends to stay withdrawn during the day. Moreover, the reflex is more efficacious in strong light: a greater proportion of animals respond and a smaller intensity change produces a response at greater light intensities (in these experiments, intensities above about 80 lux were most effective).

It is not certain to what depths in the sublittoral zone *Branchiomma* descends. Locally, in the Salcombe estuary (South Devon), it is found on the lower shore at low spring tide level, and slightly above. The tidal range in this estuary is 17·3 ft. (Evans, 1947). Absolute values for submarine light intensities are not available for the Salcombe estuary, but Atkins (1945) has summarized information for coastal and inshore waters near Plymouth. At a depth of 5 m., transmission of light would be reduced to about 10 % of subsurface illumination. This would permit bottom illuminations of about 5400 and 1800 lux at high-water springs on clear days in June and December respectively. Higher intensities would be encountered of course as the animals approached emergence during low water. In somewhat turbid water maximal transmission occurs in green light, and transmission decreases somewhat in the blue, and markedly in the red (Atkins, 1939, 1945; Atkins & Poole, 1940). In conjunction with this information we may observe that *Branchiomma* is sensitive to light in all parts of the visual spectrum (blue to red, 4000–7000 A.), but is more sensitive to light of short and medium wave-lengths, than to red light.

Most workers on the behaviour of tubicolous polychaetes have considered only the withdrawal or giant axon reflex. This reflex must have considerable survival value in terms of predation-pressure. Light can be one sensory modality eliciting this response, but for various sabellids and serpulids, light influences the character of other responses as well. Protrusion of the branchial crown in light and darkness has already been considered; the influence of light on this activity varies in two species of sabellids (*Branchiomma* and *Sabella*). The orientation of the branchial crown and anterior end of the tube towards the light would ensure that the feeding organs were directed towards the open, when the animals were in confined surroundings. This response is of particular interest since the effectors concerned in orientation of the tube appear to be glands in the body wall (Loeb, 1906; Fox, 1938). Finally, *Branchiomma*, divested of its tube, executes locomotory movements in which light has a directive value, and which lead it into darker regions.

Summary

In *Branchiomma vesiculosum* decrease in light intensity causes the animal to contract and withdraw into its tube. A decrease, never an increase, in illumination is the effective stimulus. When repeatedly stimulated the animals quickly become adapted to intensity changes and no longer respond.

The minimal effective intensity change has been determined for a range of intensities. $\Delta I/I$ is found to increase in low light intensities, and to be fairly constant in intensities over 50 lux. The animals are least sensitive to red light; sensitivity increases in shorter wave-lengths.

Animals show considerable sensitivity in weak light. They respond to intensity changes in illumination at least as low as one-third of a lux. Animals kept under undisturbed conditions show enhanced sensitivity and responsiveness. Frequent stimulation raises the stimulation-threshold and establishes a lasting state of habituation.

Animals respond both to a sudden diminution of illumination and to a moving intensity change. Adaptation to the former does not necessarily abolish response to the latter, which shows an independent course of adaptation.

Branchiomma protrudes its branchial crown in light and darkness.

Tubes and branchial crowns are directed towards the light (positive phototropism).

Branchiomma, removed from its tube, shows negative orientation to light in its locomotory movements (retrograde creeping). Animals congregate in dark places.

The sensitivity and responses to light are discussed in terms of the life habits of the animal.

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THE REPRODUCTION AND LARVAL DEVELOPMENT OF *NEREIS DIVERSICOLOR* O. F. MÜLLER

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(Plate I and Text-figs. 1–13)

CONTENTS

	PAGE
Introduction	321
Methods	322
Reproduction	323
Sex ratio	323
Differentiation of the sexes	324
Changes occurring at maturity	324
Colour changes	327
Maturation and structure of the oocytes	328
Maturation and structure of the spermatozoa	329
Parasites	330
Spawning mechanism	330
Conditions governing the time of spawning	332
Duration of spawning season	333
Larval development	335
Early development	335
Later development of the free-swimming larva	337
Development of the jaws and chaetae	343
Elaboration of the parapodia	345
Development of the head region	345
Larval habits and life history	347
Growth of the larvae	349
Comparison with other accounts of nereid larvae	351
Comparison with larvae previously ascribed to *Nereis diversicolor*	352
Discussion	353
Summary	355
References	356
Appendix: Tables VI and VII	360

Introduction

It is somewhat surprising that although *Nereis diversicolor* O. F. Müller is one of the commonest of all shore polychaetes in the British Isles and north-western Europe, its early development has hitherto been unknown. The species has, however, attracted considerable attention and many divergent views have been expressed about its reproductive habits.

The present paper presents a reasonably complete account of the larval life history, and also a discussion of the diverse views expressed about various aspects of its reproductive habits.

The most interesting points discussed, apart from the development of the larvae in the mud, are the existence of a form of pseudo-copulation, the absence of an epitoquous stage, and the general absence of the phenomena of hermaphroditism (Mendthal, 1889), parthenogenesis (Schultze, 1856; Herpin, 1923*a*, 1925, etc.), and viviparity (Schröder, 1886; Gravier, 1905; Benham, 1910; MacGinitie & MacGinitie, 1949) previously attributed to the species by these authors.

I am glad to have this opportunity of expressing my thanks to Dr G. E. Newell, of Queen Mary College, for the original suggestion of the subject of this work and for constant encouragement and help during its progress, and to Dr J. E. Forrest, of Queen Mary College, for kindly reading the typescript.

Methods

All observations on breeding habits, unless otherwise stated, were made on a single population at Chalkwell, Essex, on the north side of the Thames Estuary, and the larvae figured and described were collected from the same part of the beach, which for convenience was near the upper limit of the intertidal flats.

Artificial fertilizations were successfully carried out by opening the coeloms of males and females and mixing the ripe gametes in shallow glass dishes. A minimum admixture of blood was obtained by slitting or puncturing the body wall at the bases of the parapodia, where it is relatively thin. The oocytes did not spurt out under pressure of the coelomic fluid on puncturing the body wall as in many polychaetes, and fairly extensive slitting was found necessary to obtain an appreciable quantity of oocytes. Sperm was more easily obtained, and sufficient quantity to fertilize a Petri dish full of oocytes could be obtained by pricking a single parapodium. Surplus sperm was washed off the oocytes after fertilization had taken place. Decantation was relatively easy as the oocytes are appreciably heavier than sea water. The fertilized eggs were found to develop well, as far as young chaetigerous larvae, if allowed to remain in shallow dishes in which the sea water was changed daily, no further attention being required.

Larvae were obtained from the mud by digging trenches through areas in which the worms were most numerous, stirring the sea water which percolated into the trench, well rinsing the overturned mud containing the adults back into the trench, and then passing this water through a fine silk net. This method which has been used to collect larvae of other polychaetes, is described by Newell (1949), and is fairly efficient when the larvae are numerous. On return to the laboratory, the water containing the larvae was poured out into Petri dishes and the silt allowed to sediment out. The larvae were then searched for under a binocular microscope, and picked out with a fine pipette.

Drawings were made with a camera lucida, those of larvae having been made from typical living specimens temporarily narcotized with a drop of 8 % magnesium sulphate and examined without a cover-glass. When larvae are left in this fluid for some time, the cilia continue to beat for about 10 min. after the larvae have ceased other movements, so that the ciliary tracts may be made out fairly well. If not allowed to remain too long in the narcotic, larvae were found to revive completely when replaced in fresh sea water.

Permanent mounts of larvae either unstained or stained with borax or alum carmine in euparal or balsam revealed no more anatomical detail than in the living state. However, details of such structures as the jaws and chaetae could be seen more easily in benzyl alcohol. This medium was found most satisfactory for examination of fixed, unstained larvae, providing these were not left too long in the fluid before examination.

The larvae fixed well in 5 % formalin in sea water, after being narcotized in 8 % magnesium sulphate. They were allowed to remain in the formalin for about 2 days, and were then transferred and stored in 30 % alcohol.

Sections of adults were cut at 8 and 10 μ, after fixation in cold Bouin's fluid, and stained with Ehrlich's haematoxylin with eosin as a counterstain.

The beach temperatures shown in Text-fig. 11 were recorded by a combined maximum-minimum thermometer lying at a depth of about 10 cm. in the mud, and protected by a heavy brass cylinder loosely plugged with cotton-wool at each end.

Reproduction

Sex Ratio

McIntosh (1907), at St Andrews, found that the great majority of individuals examined in December were females; and Dehorne (1925) also notes that the number of females is greatly in excess of the males. Schröder (1886) found three males in a sample of forty-eight (6·25 %), and Herpin (1925) found the ratio of males to females at Cherbourg to be 1 : 7 (about 14·3 %). Durchon (private communication), on the other hand, reports the males to form as much as 30 % of the population at Luc-sur-Mer. It is this scarcity of males which has been partly responsible for the suggestion that the worm reproduces parthenogenetically. It would appear from these references and from numerous observations made by the writer that this predominance of females is probably universal.

The proportion of males to females naturally varied in any one sample taken during early spring, and this was probably due to the samples being too small, since owing to the relative scarcity of the males comparatively large samples have to be taken to obtain a significant result. It is also possible that the proportion of males to females is different in different localities. At

Chalkwell, in various samples taken before spawning had taken place the percentage of males varied between 1 and 10 (3 in 35, 5 in 153, 3 in 218, 4 in 109, 9 in 138).

Differentiation of the Sexes

In the autumn the sexes are externally indistinguishable, although by October the coeloms of the females contain small oocytes and the sexes may be determined by slitting open the body cavity. The oocytes at this stage are rather small (100 μ) and cannot be seen without the aid of a good lens.

In summer and autumn all the worms assume a reddish brown colour, but in early spring become bright green. The mature males have a bright grass-green colour and may thereby be distinguished from the females, which have a much darker green colour which is often lacking on the ventral side at this stage. The ripe males, that is, males containing free sperm, are completely green, and the red and brown pigments, which are usually still recognizable in the ripe female, cannot be seen in the male. The white mass of sperm which by then packs the coelom of the male gives the sex its lighter green colour, and when the sperm has been shed the males are appreciably darker in colour.

Apart from colour differences, the mature female may be recognized on the shore by slightly stretching the animal between the fingers when the oocytes, which by then are quite large (200 μ) and visible to the naked eye, may under favourable conditions be seen moving with the coelomic fluid.

In many nereids the males when mature may be distinguished by the development of an anal rosette, the sperm being discharged through the anus after histolysis of the gut (Gravier, 1923 *a*). This does not appear to be so in *N. diversicolor*, and no anal rosette could be distinguished in mature or spawned males.

Changes Occurring at Maturity

Most recent authorities agree that *N. diversicolor* is typically atoquous. Changes, or instances of partial metamorphosis (i.e. change of body form as a preliminary to spawning usually resulting in a free-swimming epitoquous or 'heteronereid' phase) which have been described may be regarded as atypical or exceptional; while the occurrence of completely epitoquous forms ascribed to this species is probably due to a confusion of species. These problems are considered in more detail in the discussion.

Although the process of metamorphosis of normal individuals into an epitoquous form is normally lacking in *N. diversicolor*, some well-marked changes do, however, occur. Thus, early in the development of the female germ cells, the coelom becomes filled with a large number of coelomic corpuscles which eventually come to form a very loose parenchyma or pseudo-tissue. Claparède (1868) was one of the first to comment on this phenomenon which since then has received attention from several workers, especially Romieu (1921 *a*, *b*), Dehorne (1922 *a*, *b*, 1924, 1925), Herpin (1921, 1925) and

Thomas (1930*b*). McIntosh (1907, 1910) also refers to the formation of this loose 'ovigerous tissue' as being possibly derived from the dorsal organ of Goodrich, and becoming attached to the vessels and the bases of the parapodia. He also notes an increase in the vascularity of the gut in December and that, when the oocytes become free in the coelom, masses of coarsely granular cells appeared sometimes in lobular masses in the region of the dorsal ciliated organ. He considered these masses of cells to be correlated with the growth of the oocytes. Herpin (1925) found, in individuals in which the sexual products were in an advanced state of development, that the coelomic corpuscles (*éléocytes*) contained fusiform bodies which were in fact fragments of muscle fibre. These *éléocytes* (he remarks) evidently have the same role as in nereids, which metamorphose at the breeding season into 'heteronereids', that is, in becoming actively phagocytic and digesting the muscle which undergoes histolysis towards maturity. This phenomenon has been studied by Romieu and Dehorne primarily in *Perinereis cultrifera*, but also in *Nereis diversicolor*. In the four papers mentioned above, Dehorne made a close study of these changes and found that there was no doubt that the spindle-shaped bodies in the phagocytes were in fact muscle fibres. He pointed out (1922*a*, *b*) that this process of phagocytosis is probably not due to a precocious invasion of the tissues by the phagocytes, but that it is more likely a result of the muscle fibres breaking up spontaneously, and their fragments then being taken up by the cells. This process is carried out over a fairly prolonged period, and the phagocytes may be regarded as specialized coelomic corpuscles.

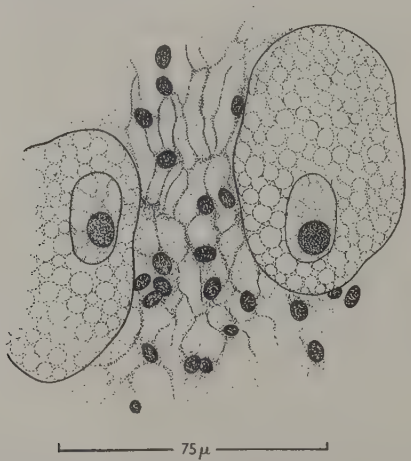
Two phases of activity of the coelomic corpuscles may therefore be distinguished. These phases, pointed out by Dehorne (1924), were identified in the Chalkwell population.

(i) Coelom filled with a heterogeneous mass of cells. (Referred to as 'parenchyma' in the present paper, and equivalent to Claparède's 'tissue connectif', McIntosh's 'ovigerous tissue', Kükenthal's 'lymphoiden Zellen', Heinen's 'Protoplasmaschicht' and Schneider's 'blasigen Gewebes'.) The formation of this loose parenchyma is presumably correlated with the development of the female germ cells, for its cells appear to be largely responsible for the deposition of yolk in the oocytes (Kükenthal, 1885; Schröder, 1886; McIntosh, 1907, 1910; Herpin, 1925; and also in *Perinereis cultrifera*; Romieu, 1921*a*, *b*). According to Dehorne the nuclei of the oocytes during this early stage are rather irregular in shape, and most of the coelomic corpuscles remain in the region of the dorsal ciliated organ. The muscles remain intact.

(ii) This loose coelomic parenchyma disappears. The mature oocytes come to fill most of the coelom, and histolysis of the muscle layers begins. The nuclei of the oocytes are now spherical and the coelom contains, apart from the oocytes, fragments of muscle fibre and phagocytes.

This gradual digestion of the muscle layers by the phagocytes enables the

oocytes to be released by the splitting of the body wall, which has become very thin by the time that spawning is ready to take place. In the specimens of *Nereis diversicolor* from Chalkwell, however, the degree to which histolysis had proceeded at the onset of the spawning period was rather variable, and was not readily detected even in some apparently mature females. Generally, however, the worms were abnormally fragile in early spring some time before spawning, and this was presumably due to the histolysis of the body-wall muscles described above. Sections of some adults showed almost complete histolysis in some instances, but in others reduction in the muscle layers was hardly noticeable. The appearance of the coelom during these various phases is shown in Text-fig. 1, and Plate I, figs. 1, 3–5. Histolysis of the muscle layers is also referred to by McIntosh (1907, 1910).



Text-fig. 1. Young coelomic oocytes. Young oocytes are seen imbedded in the parenchyma.

Thieren (1909) concluded that this histolysis is caused by unfavourable conditions and insufficient oxygen supply, and that breaking down of the tissues occurs where the oxygen consumption is normally highest; and also that this, in *N. diversicolor*, facilitates spawning before the assumption of an epitoquous stage is completed by the individual. He suggested that histolysis may also be caused by internal secretions, or as a corollary of normal metamorphosis. Thieren's suggestion, however, that spawning takes place before metamorphosis into an epitoquous stage has begun, thus explaining the atoquous habit, cannot be supported since no further change appears to occur in unspawned individuals in which the oocytes eventually break down, and which usually die off before the next winter without showing any signs of

metamorphosis. Dehorne (1922*b*), indeed, concludes that as phagocytosis occurs in *N. diversicolor* which is atoquous, the process may be regarded as independent of metamorphosis.

In the male, the first phase in the activity of the coelomic corpuscles, that is the formation of a loose parenchyma, is of very short duration, and this supports the hypothesis that the formation of the coelomic matrix in the female is concerned mainly with the growth of the oocytes and the deposition of yolk. On the other hand, histolysis occurs in the male as well as in the female, and often appears to be taken much further in the male. The relation of this to spawning is discussed below.

Colour Changes

The colour change occurring at maturity is one of the most interesting aspects of the reproduction of this species, and has been noted by several previous workers (Mendthal, 1889; de St Joseph, 1906; McIntosh, 1907, 1910; Herpin, 1923*a*, 1925; Dehorne, 1925; Thomas 1930*a*).

Mendthal considered this green colour to be due to a diet of green algae. McIntosh, however, who also found green females in January, rejected this explanation and concluded that this colour was due to the presence of 'pale greenish ova', yet he states that the sexes are not always distinguished by colour differences and reports finding both males and females of a greenish or dull yellowish colour, of which the males were usually paler. McIntosh offers no explanation of the cause of the coloration in the male sex; but his general observations on the slight colour differences between the sexes are in accordance with the observations made at Chalkwell.

The coloration of *N. diversicolor* is being investigated, and as it is hoped to publish the results separately, only a brief outline of the process of colour change is given here. In either sex the assumption of the green coloration occurs about the same time as the onset of histolysis, the phagocytes in the coelom being richly charged with granules of a bright green pigment which later becomes deposited under the cuticle. This general green colour is apparently correlated with maturity, and at Chalkwell the percentage of green worms rose steadily to practically 100 % just after the main spawning period, afterwards dropping steadily during early summer. In December, for example, only a very few green worms were found; in late February and March, on the other hand, practically all the worms were green; while by the end of May only very occasional specimens bore traces of green pigment. Such individuals were invariably found to contain mature oocytes in contrast with those with a reddish brown colour, which were either empty or contained a milky fluid formed from broken-down oocytes. This correlation was found to be statistically significant. The females appear to lag behind the males slightly in assuming the green colour. No support was found for the explanations of the presence of green pigment made by Mendthal or McIntosh.

It is also interesting to note here that *N. japonica* which appears to be closely related to *N. diversicolor*, and with which it was originally confused, also becomes green at maturity (Izuka, 1908), although, unlike *N. diversicolor*, *N. japonica* possesses an epitoquous phase.

Maturation and Structure of the Oocytes

Schröder (1886), Mendthal (1889), Schneider (1902), and Heinen (1911) agree that the female sex cells arise in the ventral region of the body in relation to the ventral vessel and between the bases of the parapodia, and it was confirmed that the germinal epithelium appears to proliferate in the ventral part of the coelom in the septal region in the worms collected at Chalkwell. The cells which eventually divide to form the female germ cells, however, break loose into the coelom at a very early stage.

Table I. Measurement of Oocytes

Size (μ)	Sept. 1949	Oct. 1948	Nov. 1948	Dec. 1948	Jan. 1949	Feb. 1949	Mar. 1949
0–25	—	—	—	—	—	—	—
25–50	—	—	—	—	—	—	—
50–75	3	4	—	—	—	—	8
75–100	6	5	—	—	—	—	1
100–125	28	32	—	—	—	—	—
125–150	13	19	—	—	—	—	—
150–175	8	56	32	8	—	—	—
175–200	—	7	46	41	4	5	4
200–225	—	1	21	46	38	14	11
225–250	—	—	5	7	80	59	51
250–275	—	—	—	—	19	24	17
275–300	—	—	—	—	1	17	9

McIntosh (1907, 1910) noted that the size of the oocytes was somewhat variable, but these oocytes from St Andrews were much smaller than those collected from Chalkwell. McIntosh gives the diameter of a mature oocyte as 152·4 μ. Herpin (1925) found the maximum oocyte size to lie between 200 and 250 μ, and emphasizes that the size variation is much more variable in *N. diversicolor* than in other nereids, noting that the mature oocytes may have a diameter of less than 200 μ. This is confirmed by Durchon (private communication), who found the diameter to vary between 190 and 240 μ. The size of the mature oocytes at Chalkwell varied between about 200 and 275 μ in diameter, the mean oocyte size at the time of spawning being about 220 μ. The actual range in size of coelomic oocytes is shown in Table I.

The coelomic germ cells in the female are first recognizable in young worms about 7 cm. in length, when they are at least 6 months old. Dehorne (1925), it is true, found oocytes free in the coelom of worms only 5 cm. in length, but it is likely that these would actually appear longer if measured after narcotization with 10 % magnesium sulphate as here employed.

Apart from the first few segments in the pharyngeal region and the most posterior segments, oocytes may be found throughout the length of the body.

At Chalkwell, samples of worms were taken throughout the year and about twenty specimens randomly selected. A few oocytes were taken from each, and about 100 measured. The range in size is shown in Table I. The mean oocyte size was calculated and was found to increase steadily over the winter months, reaching a constant maximum size rather before the main spawning period. This provides a useful method of prediction of spawning time, as pointed out by Newell (1948, 1949). Oocytes were found in the coelom from early September to early May, but were absent during the summer months.

When mature, the oocytes come to fill the main body cavity and the spaces in the parapodia, frequently becoming crushed together. On slitting open the coelom of a mature female the oocytes which are released are often dented and rather irregular in outline through being crammed together, but when not dented are practically spherical. On contact with sea water they quickly round off. They are a very pale straw colour, and not pale green as noted by McIntosh (1907). A large central germinal vesicle is surrounded by a highly granular cytoplasmic area composed of rounded yolk globules (Text-fig. 1).

The larger oily droplets observed in some other species of *Nereis* (E. B. Wilson, 1892; Herpin, 1925; D. P. Wilson, 1932, etc.) are not visible in *N. diversicolor*. This may be correlated with the typical bottom development of the larvae of this species, since these droplets appear to occur in typically pelagic nereid larvae.

After the spawning period has passed, the oocytes in the females which have not spawned gradually break down into a white milky mass in the coelom, the observations made by the writer being in accordance with those made by McIntosh (1907). Oocytes remain in the coelom for nearly 2 months after the main spawning period before finally breaking down. Thomas (1930*b*) found that the oocytes were invaded by a chromolipoid pigment, the cytoplasmic constituents disappearing, the corpuscles becoming actively phagocytic, and surrounding the degenerating oocytes during this process.

Maturation and Structure of the Spermatozoa

In the male the loose parenchyma is transitory, and the sperm mother cells, which presumably originate from the coelomic epithelium in much the same position as the oocytes, break away into the coelom in small groups. These 'sperm plates' as they may be called, are very characteristic flattened groups of cells found in many polychaetes, though differing much in size and appearance in different species. In *N. diversicolor* at Chalkwell they were found in the coelom from December until February. The number of cells in each plate or disk increases with age, but free spermatozoa are not formed until the normal breeding season is reached. The young sperms acquire their tails while still attached to form a sperm plate, but soon after they break away

into the coelom. Males containing mature sperm were found for some 2 weeks before spawning apparently took place.

The ripe spermatozoan (Text-fig. 4) bears a sharply defined acrosome anteriorly, and a tail about 40 μ in length posteriorly.

Parasites

In a very large proportion of the males found at Chalkwell the coelom was found to contain quantities of a single form of unidentified ciliate which apparently fed on the spermatozoa. The amount of sperm left by the time the spawning period was reached was negligible in some instances, and in these the general body cavity and parapodial spaces were crammed with ciliates.

Spawning Mechanism

Unfortunately, in spite of much observation, spawning was observed neither under natural conditions on the shore, nor in the laboratory.

There are theoretically four ways in which the germ cells may be released from the coelom: (1) through the nephridia; (2) by the coelomic ducts (ciliated organs) acquiring openings to the exterior during the breeding season; (3) through the anus after histolysis and perforation of the gut; (4) by rupture of the body wall.

Release of the Oocytes

The first of these methods was maintained by Mendthal (1889), though the oocytes are manifestly too large for it to occur. Regarding the second method, Benham (1910) suggested that the ciliated organs might acquire openings to the exterior, but this may be discounted in light of recent work by Goodrich (1945). Goodrich, however, was obviously not convinced or did not realize that *N. diversicolor* is atoquous, since he suggested that atoquous nereids might have functional ducts. This has not been found to be so. Regarding the third method, it may be assumed that it is extremely unlikely that oocytes would ever be discharged through the anus. Release of the oocytes by rupture of the body wall has been observed by Herpin (1925), who describes the shedding of oocytes as being preceded by contraction of the posterior end of the body. McIntosh (1907) also expresses the opinion that they are shed by this means, and this is confirmed by Durchon (private communication).

Emission of the Spermatozoa

As in the female there is no evidence that the ciliated organs acquire openings to the exterior, nor is there any evidence that the sperm is discharged through the anus, since spawned males appeared to have the gut intact, showed no sperm in the gut, and lacked the anal rosette which is developed in *Perinereis*

marionii (Herpin, 1923*a*; Gravier, 1923*b*), *P. cultrifera* (Herpin, 1923*b*; Gravier, 1923*a*; Gravier & Dantan, 1928) and other species.

As a few spawned males which showed no signs of damage to the body wall were found in late February, the sperm is almost certainly discharged through the nephridia, though in some instances emission may accidentally occur by rupture of the body wall.

General considerations

In the laboratory, apparently, fully mature females could not be induced to spawn in the presence of males, whether placed in glass dishes or in the aquarium in fresh sea water under various conditions of light and temperature; nor in the presence of motile sperm from ripe males. Conversely, ripe males could not be induced to emit sperm when placed together with ripe females, ripe oocytes, or in 'egg-water' from crushed ripe oocytes. Other workers seem to have been rather more successful in this respect with this somewhat temperamental species. Herpin (1925) watched ripe females spawning under laboratory conditions. Just (1940) also found at Roscoff that mature individuals released their gametes into dishes in the laboratory during January and February, and this writer was apparently successful in making artificial fertilizations with these naturally spawned gametes, and in rearing the larvae for 3 months afterwards. Unfortunately, no details are given of the subsequent development, nor is it stated whether the males and females spawned in separate dishes or together, or how this spawning actually took place.

Under natural conditions Dehorne (1925) described a kind of copulation or sexual congress, in which several females were found coiled round a single male. Müller (1771, see Dehorne, 1925) had also apparently seen tangled masses of worms under stones and compared them with tangled masses of macaroni. Dehorne regards this observation of Müller's to have been similar. Herpin (1925) also found males and females coiled or knotted together posteriorly and more or less agglutinated with mucus on the surface of the mud, a condition known locally as 'Roi de rats'. This knotting together is not, of course, specifically related to reproduction, and may be observed in the laboratory whenever too many individuals are confined together in a tank, and Durchon (private communication) also concludes that this is probably a purely accidental phenomenon. Herpin supports Dehorne's conclusion that a form of sexual congress occurs in which clusters of females come to surround a single male. Herpin concludes that the ripe females swim in search of the males during the night, and that a tangle of females forms round each male, the oocytes being gradually released and fertilized by the sperm emitted by the male.

Dehorne (1925) also mentions that the females are positively attracted by the secretions of the male, and that when in contact provoke the emission of sperm. He points out that usually, as in epitoquous nereids, it is the males

which stimulate the females to release their oocytes, but here, owing to the rarity of the males, the reverse seems to occur. Thorson (1946) states that it may be regarded as a general ecological rule that it is the males which stimulate the females, but he notes that there are exceptions. Galtsoff (1940), for example, found in *Gryphaea virginica* that though chemical stimulation was specific for females, this was not so for males. Townsend (1939), confirming the 'fertilizin' theory of Lillie, and Just (1930*a*, *b*) found that the reaction of the male of *Nereis limbata* was extremely specific to glutathione which is present in the unfertilized oocyte, and this appears to be fairly general, though no experiments appear to have been performed on *N. diversicolor*. Although Dehorne concludes that this species is an exception to the general rule in relation to the comparative rarity of the males, it does not necessarily follow from this fact that it is the females which seek out the males and prompt spawning. It may well be that having come in contact with a male by chance or by attraction by some other stimulus, it is the male which actually initiates the simultaneous emission of the gametes.

Conditions Governing the Time of Spawning

At Chalkwell, spawning took place in 1949 within 2 weeks centred around the third lunar quarter in late February. At this time both males and females had apparently been mature for about 2 weeks. At the time of spawning a sharp rise in temperature occurred. Authorities seem to differ as to the actual time of year when spawning takes place, but this is discussed later.

The fact that the spawning period centred round the third lunar quarter is interesting in that it is at this phase that many epitoquous nereids spawn. Whether this is in fact a lunar effect, in *N. diversicolor*, is not known, and can only be determined after study for a number of years. This problem has been given much attention by Fox (1932) and by Amirthalingham (1928), who concluded that apparent correlation with lunar phase was due to several practicably inseparable effects. It is worth noting, however, that Newell (1948) found a correlation with a lunar phase at which spawning took place over a sharply defined period, in the common lugworm *Arenicola marina*, whose habitat is not widely different from that of the species under consideration.

Although factors relating to the lunar effect may possibly be correlated with the growth of the gametes, the actual stimulus required to initiate spawning is frequently the attainment of a definite threshold temperature or temperature change (Orton, 1920; Thorson, 1946). At Chalkwell, as already mentioned, spawning took place at a time when there was a marked rise in temperature, and may have been stimulated in this way. The temperature during the week when the main spawning took place varied between 5 and 8·8° C.

From a study of size distributions of adult populations obtained from various stations on British coasts, it may be concluded that spawning generally takes place in early spring, and the fact that McIntosh found spawning to take

place in east Scotland about a month later than the writer found in southern England again suggests that a threshold temperature may be the factor initiating spawning.

Duration of Spawning Season

The variability of the reproductive habits within a single species of nereid is notorious, and this, together with the possibility of confusion of the species of *Nereis* to which the various larvae have been ascribed, makes it difficult to assess the value to be attached to reports of *N. diversicolor* larvae occurring at widely different seasons of the year. Information from various sources which throw light on these points is summarized in Table II.

TABLE II. BREEDING PERIOD OF *NEREIS DIVERSICOLOR*

Author	Locality	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Present paper	Chalkwell, England	O	O, S	O, L	O, L	—	—	—	—	O	O	O	O
McIntosh	St Andrews, Scotland	O	O	O, S	—	—	—	—	—	—	O	O	O
Thamdrup	Skallingen	—	—	O	O	O	O	O	—	—	—	—	—
Just	Roscoff	S	S	—	—	—	—	—	—	—	—	—	—
Smidt	Copenhagen	—	—	—	L	L	L	L	L	L	L	L	—
Herpin	Cherbourg	S	S	S	S	S	S	S	S	S	S	S	S
Nunn	Plymouth	—	—	—	O	—	—	—	—	—	—	—	—
Hofker	Zuidersee	—	—	—	—	—	—	L	L	—	—	—	—
Thorson	Øresund	—	—	L	L	L	L	L	L	—	—	—	—
Blegvad	Nyborg	—	—	—	O	—	—	—	—	—	—	—	—
Mendthal	B. of Pillau	—	—	—	—	—	O	—	—	—	—	—	—
Durchon	Luc-sur-Mer	—	S	S	S	—	—	—	—	—	—	—	—

O = oocytes in the coelom; S = spawning; L = occurrence of larvae.

Thorson (1946) points out that the length of the breeding season of any marine organism may depend on three main factors. With reference to *N. diversicolor* these may be summarized as:

(i) Vertical distribution on the shore, with resulting effects, *e.g.*, a graded temperature, so that a possible optimum spawning temperature will be reached progressively later at greater depths.

(ii) Variation in the time taken by populations or individuals to mature.

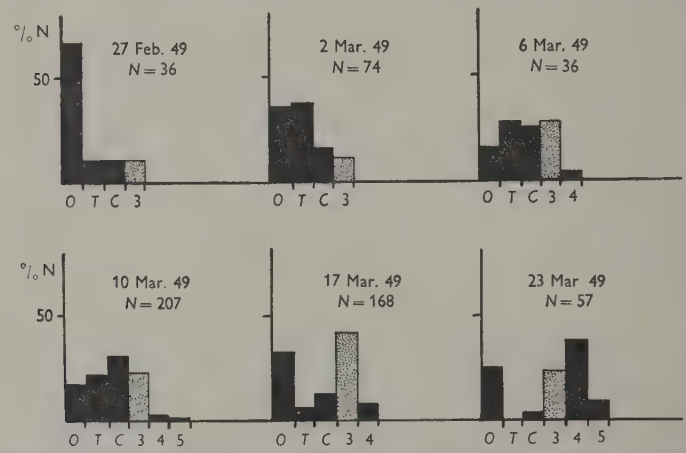
(iii) Repetition of spawning by the same individuals within one season, or protraction of spawning over a period.

The first factor seems most likely to promote an extended breeding season, Herpin (1925) regards this and the variability of habitat to cause spawning to take place all the year round at Cherbourg. Also, if this occurs together with migrations of individuals between the levels, the breeding season may actually be extended at any one locality.

With regard to the second factor, it may be noted that a small number of individuals of both sexes are sometimes slow in maturing. In late summer one or two mature worms may be found, and these may be successful in spawning. Usually these late maturing females are so few that the chance of coming in contact with a ripe male is remote, but the possibility remains, especially when the number of males is relatively high.

The third effect is not found in this species. Individuals die soon after spawning, and unspawned worms may last only the summer, for the length of life does not appear to cover more than one breeding season. Also, in any one worm the gametes are all much in the same state of development, which suggests that the spawning period is restricted. McIntosh (1907, 1910) found females in January and February which he considered to have partially spawned, but these may have been immature worms.

As already noted, spawning at Chalkwell took place between 13 and 27 February, and from that time onwards larvae were obtained from the natural habitat in sufficient numbers to make quantitative counts of the



Text-fig. 2. Histograms of relative numbers of larvae at various stages. *O*, unfertilized oocytes; *T*, trochophores; *C*, early chaetigerous larvae; 3, 4, 5 larvae with three, four or five chaetigerous segments respectively.

various larval stages possible. The numbers of larvae at different stages are represented as percentages of the total on each date, and shown as a series of histograms in Text-fig. 2. These represent counts of larvae taken at 3-day or weekly intervals, up to a month after the main spawning date. Further samples were taken, but these merely show a steady drift along the abscissa. Larvae were not found later, in summer. The diagrams also show that some oocytes continue to be discharged into the sand after the spawning period, but owing to the absence of males or for some other reason, these were not fertilized. In artificial fertilizations unfertilized oocytes retained their original appearance and showed no signs of degeneration for as much as 10 days in fresh sea water, but it seems unlikely that even in the natural habitat oocytes would remain in a healthy state for as long as 5 weeks. Presumably these are released accidentally by unspawned females.

Larval Development

Early Development

Early development seems to follow the general plan already described for other species. Cleavage is spiral and is dextrorotatory, as described by Wilson (1892) for *N. limbata* and *N. megalops*. The thick gelatinous envelopes described in these and other species (Herpin, 1925) are not always present in *N. diversicolor*.

The early development was followed from artificial fertilizations. Fertilization membranes are thrown off between 0·5 and 2 hr. after mixing the gametes (Text-fig. 3). The membrane gradually crumples off the surface of the egg and eventually stands away from its surface at a distance which varied in different fertilizations (Costello & Young, 1939) and with gametes at different stages of maturity.

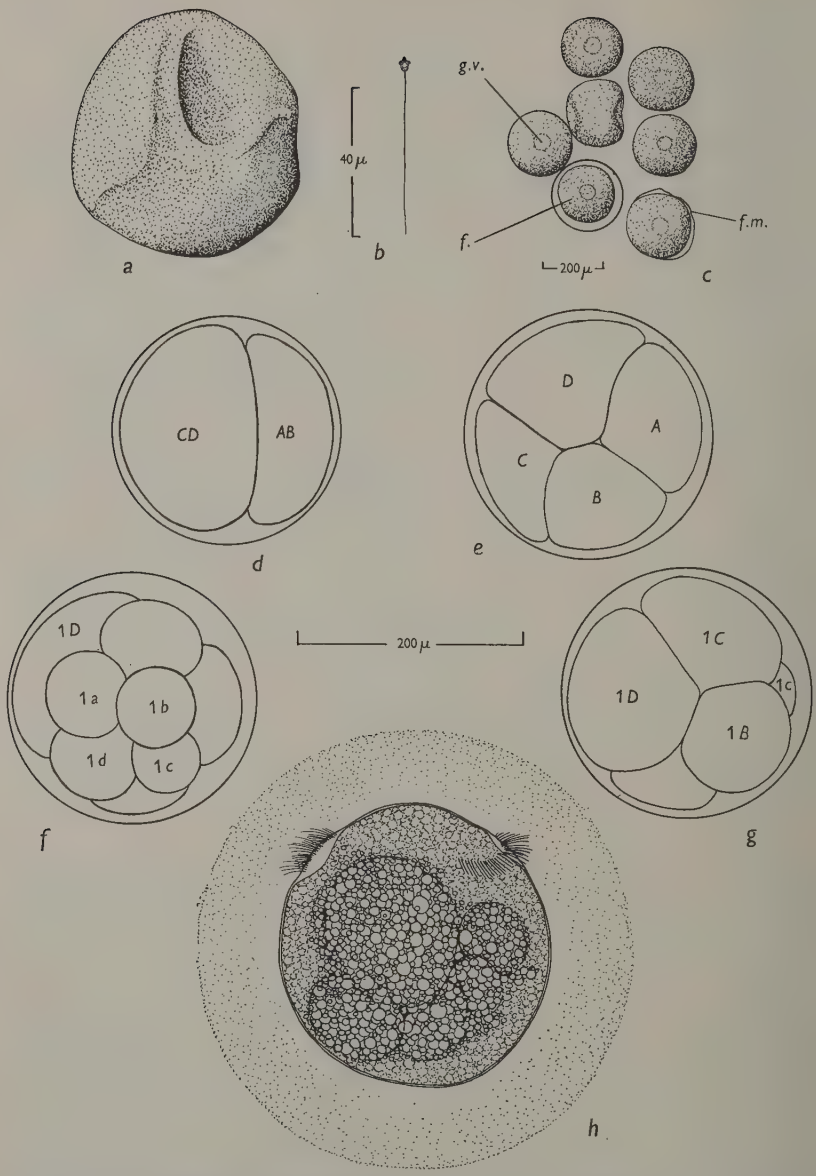
A jelly layer was sometimes extruded after fertilization, and was clearly visible by the time the later cleavage stages were reached owing to the adhering sperm and bacteria. These layers were apparently absent as a rule, and were never seen in nature surrounding cleavage stages or young trochophores.

In cleavage, the *D*-cell of the 4-cell stage was not much larger than the other three blastomeres, and in early cleavages obtained from fertilizations in late January and February (1949), the *D*-cell was not very distinct. Cleavages with immature gametes were generally more or less irregular, so that no well-defined cleavage pattern was discernible. However, the pattern approximated more nearly to the spiral type, with recognizable quartettes of micromeres as the spawning period was approached.

Polar bodies were very small, and owing to the yolky nature of the egg were difficult to detect. Cleavage times varied in different fertilizations but were generally slow, as compared with some other species of *Nereis*. The cleavage stages figured were drawn 20 hr. after fertilization but represent different phases of development.

Quartettes of micromeres became cut off and spread over the remaining megameres which could be seen rather indistinctly lying in the centre of a ball of cells forming the gastrula. The number of megameres remaining varied slightly, and although later larvae had usually only 4, 5 or 6 were visible in the monotrochophore.

When the larva begins to rotate, cilia are not visible. Cilia are not easily distinguishable until about the fourth day after fertilization. At first the rotary movement appears to be inside the fertilization membrane, but when the cilia begin to grow out near the animal pole, they appear to penetrate the fertilization membrane, which then becomes the larval cuticle. As a rule, rotation begins about 3 days after fertilization, but in some of the earlier artificial fertilizations the larvae began to rotate as early as the 16-cell stage. At first rotation is never continued for periods of more than a few seconds, separated



Text-fig. 3. *a*, unfertilized oocyte on release from coelom; *b*, spermatozoan; *c*, spawned eggs (*f*, fertilized egg, *f.m.*, fertilization membrane, *g.v.*, germinal vesicle); *d*, 2-cell stage; *e*, 4-cell stage; *f* and *g*, 8-cell stage, seen from animal and vegetable poles; *h*, young monotrochophore with jelly layer. The scale in the centre applies to all except *b* and *c*.

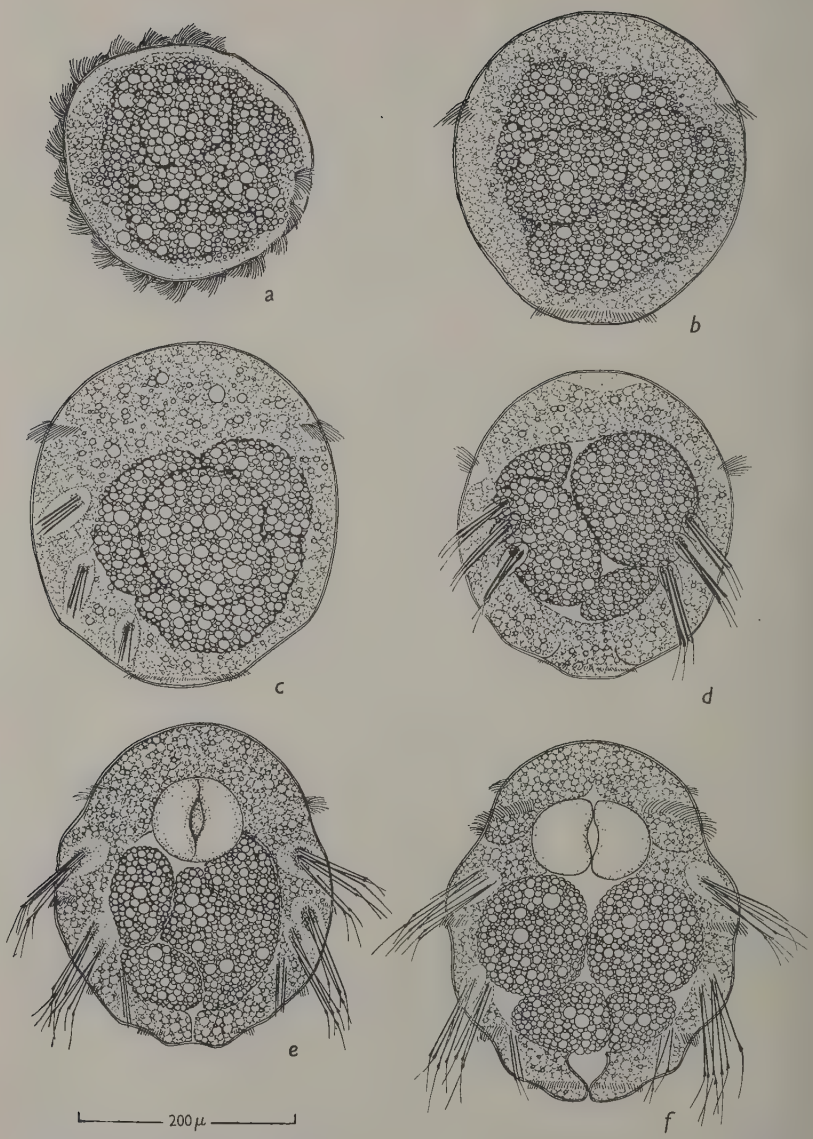
by long pauses, but as the larva develops it becomes more vigorous and is continued over progressively longer periods.

At the beginning of the fourth day after fertilization only one large tuft of cilia may be seen in the prototrochal region. This gradually extends round the larva, but is probably never completed (Text-figs. 3*h*, 4*a*). If a jelly layer is present, the larva, which may now be described as a monotrochophore, breaks through the layer at this stage; but more usually such a 'hatching' process is absent and the gradual extension of the prototroch eventually enables the larva to swim off the bottom instead of merely rotating in one position. The degree of development of the prototroch was found to vary in different larvae.

Later Development of the Free-Swimming Larva

By the time that the monotrochal stage has been reached the larva has become free-swimming, although its swimming powers are rather limited. Soon after this it begins to elongate slightly, becoming more conical in shape and in side view a faint telotroch may be seen (Text-fig. 4*b*). This consists of very fine short cilia and probably contributes little to the locomotory powers of the larva. In many larvae it is difficult to detect, and cannot be seen without narcotization, the prototroch remaining the most important ciliary tract throughout the early larval life. When the telotroch is well developed, however, the swimming is probably better controlled, and whereas previously the monotrochophore was capable only of swimming in circles, by the time that this later stage is reached the larva can, while revolving on its own axis as before, now progress more or less in a straight line. Between four and six megameres can still be seen at this stage, and no chaetae are yet distinguishable.

Very soon after the telotroch is formed, however, chaeta rudiments become visible. Three chaetal sacs are formed simultaneously, each containing four or more rudimentary chaetae, which even at this stage are clearly compound although the distal part is very short, though this quickly elongates when the chaetae project beyond the cuticle (Text-figs. 4*c*, *d*). By the time the first three pairs of bundles of chaetae, which correspond with the first three chaetigerous segments, have come to project beyond the cuticle, the larva is about 10 days old. (Age of larvae throughout this paper is reckoned from the time of fertilization.) Very often at this stage four megameres may still be seen quite clearly, but a cavity, the larval gut, gradually comes to surround them (Text-fig. 4*d*). The chaetae are still incapable of independent movement, and the larva swims mainly by action of the prototroch. About the same time a slight invagination of the cuticle at the posterior end indicates the formation of the proctodaeum; and at the anterior end a clearer area of protoplasm devoid of any yolk granules may be seen in some larvae. This last feature is of doubtful significance, since it was only clearly recognizable in a few instances. By now the larvae have grown to about 280μ in length.



Text-fig. 4. Early stages of the larva: *a*, 'hatching stage' (viewed from animal pole); *b*, slightly later stage showing telotroch (side view); *c*, larva showing early formation of first three chaetal sacs (side view); *d*, early larva with three chaetigerous segments (dorsal view); *e*, larva with three chaetigerous segments (ventral view); *f*, slightly older larva with three chaetigerous segments (ventral view).

The young chaetigerous larva

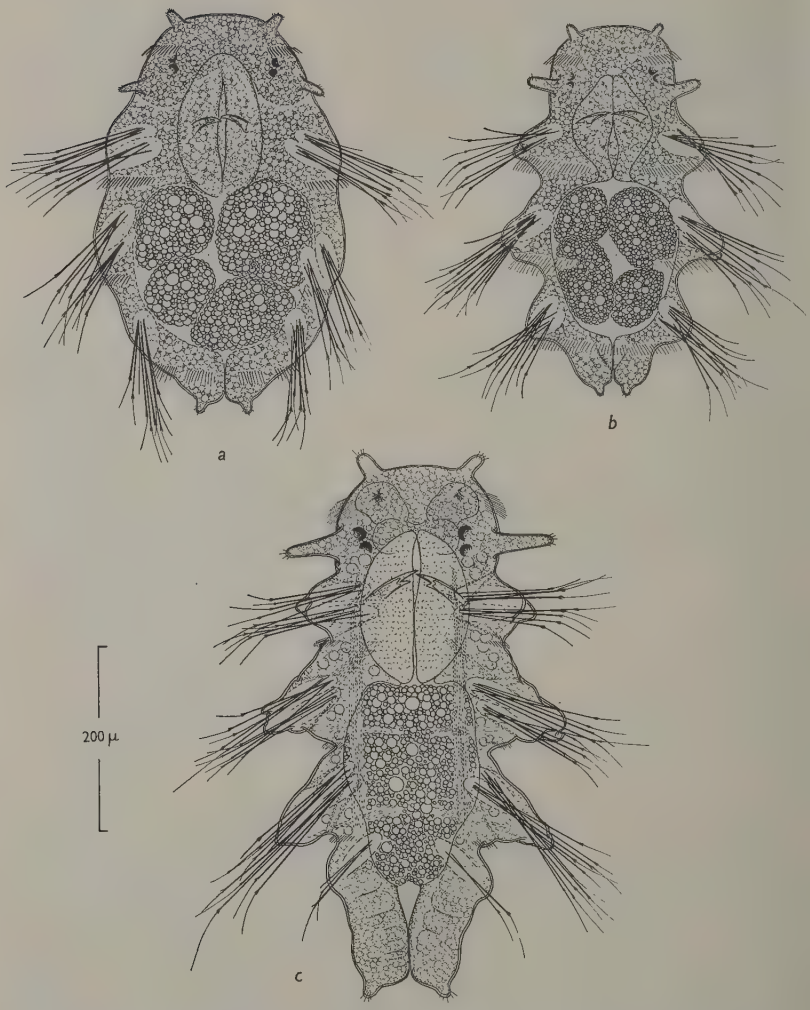
When about 2 weeks old the larvae have reached a length of about 330 μ, and may be conveniently termed 'young chaetigerous larvae' to distinguish them from slightly later larvae, which though still possessing only three chaetigerous segments, differ considerably in their external morphology, for they undergo great morphological changes before a fourth segment is added. It is thus convenient to distinguish between 'young chaetigerous larvae' and later 'larvae with three chaetigerous segments', although both stages possess three pairs of chaetal sacs. Although in the young chaetigerous larva the prototroch and telotroch remain in much the same state of development as in the earlier stages, the chaetal sacs soon acquire muscles, and the chaetae become capable of being moved. At first the chaetae in each bundle appear to arise from a single chaetal sac, but neuropodial and notopodial sacs soon become recognizable. The larval gut becomes much more highly developed, the pharynx becoming visible in ventral view as a large spherical mass of clear cells enclosing a median longitudinal cavity. The rectal region and anus can now also be seen, the four remaining macromeres still occupying most of the gut cavity.

The state of development of the different pairs of chaetae bundles is somewhat variable. Frequently all three pairs are equally developed, but in some (Text-fig. 4*e*) the third pair lag behind the anterior groups in development.

By the end of this stage a slight demarcation of the head region usually makes its appearance. Small patches of cilia may also be seen developing posteriorly to each group of chaetae, and these cilia become quite prominent in some larvae. They are usually composed of longer cilia than those of the telotroch, but are still small enough to be difficult to detect in some larvae, the prototroch remaining the only really prominent ciliary tract. Occasionally a few short cilia-like processes were detected in the apical region, similar to those figured by Wilson (1932) in *Nereis pelagica* larvae.

The Later Larva with Three Chaetigerous Segments

There is a considerable amount of differentiation during this stage (Text-figs. 4*f*, 5*a*, *b*). The rectal and pharyngeal regions of the gut become better developed and simple jaws become visible. Two pairs of simple red eye-cups appear on either side of the head region, and two pairs of short tentacle-like processes grow out from the head. The anterior pair are short and eventually form the prostomial tentacles, while the other pair, which are rather longer, form the first pair of prostomial cirri. Palps are not visible at this stage. The chaetae become more prominent and come to be borne on recognizable, though rudimentary, parapodia (Text-fig. 5*b*). Anal cirri may also be seen growing out on either side of the anus. They bear fine hair-like processes, similar to those on the prostomial tentacles and peristomial cirri, and are



Text-fig. 5. *a*, larva with three chaetigerous segments (dorsal view); *b*, larva with three chaetigerous segments, about 3 weeks old (dorsal view); *c*, larva with four chaetigerous segments, about 4 weeks old (dorsal view).

presumably sensory structures, which are also characteristic of the adult. By now the larva is about 400 μ long, and is quite active, the chaetae, which are now provided with muscles attached to the bases of the chaetal sacs, being moved fairly vigorously during swimming or crawling.

The Larva with Four Chaetigerous Segments

By the time that a fourth chaetigerous segment is becoming differentiated the larva is about 4 weeks old and is about 570 μ in length (Text-fig. 5*c*). The ciliated bands remain in much the same condition as in larvae with three chaetigerous segments, but the parapodia are becoming more complex in structure and their musculature greatly increased. The general musculature of the body wall now becomes more prominent; septal muscles are visible in the mid-gut region, and longitudinal muscles may be seen lying on either side of the gut in the dorsal region.

The fourth chaetigerous segment is represented at first by slight outpushings of the body wall, with two or three chaetae in an apparently simple sac. As in all segments during their early phases of growth, definite neuro- and notopodial sacs are not recognizable, and apparently only separate later.

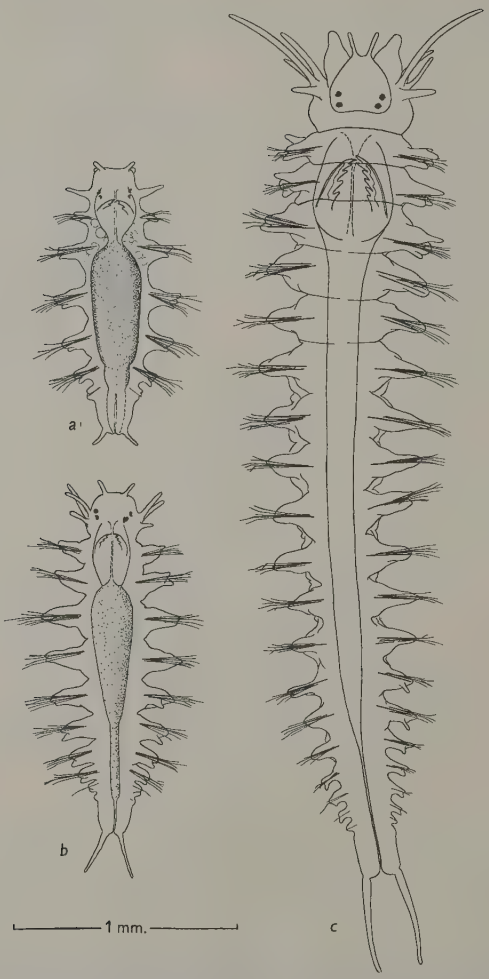
In the head region the palps are becoming more prominent, and small light pigment patches sometimes occur on the dorsal surface of the prostomium just anterior to the two pairs of eye-cups. These presumably correspond to the similar patches described by Wilson (1932) in the larvae of *N. pelagica*, where they may be quite prominent. In *N. diversicolor* larvae, however, they are never obvious and may easily be overlooked in a swimming larva, and are frequently absent. These patches are figured in the larva with four chaetigerous segments shown in Text-fig. 5*c*. They disappear later, and were never seen in larvae with five or more chaetigerous segments. The jaws become further elaborated and possess another tooth by this stage.

The megameres in the gut have by this time broken down into an amorphous mass of yolk, which still, however, fills the mid-gut region.

Later Development

By the time five chaetigerous segments have been delimited, the larva is rather over 1 mm. in length and is about a month old. The gut becomes further elaborated, the jaws growing in size and becoming armed with an increasing number of teeth. The palps grow rapidly, and the tentacles and cirri of the head region together with the anal cirri grow steadily. By this time coelomic spaces are clearly visible between the gut and the body wall, and masses of rounded cells, presumably the first coelomic corpuscles, may be seen tumbling about in the coelom with the movements of the larvae.

Larvae with six, nine and nineteen chaetigerous segments are shown in Text-fig. 6, from which it will be seen that septa become externally visible when about seventeen or eighteen segments have been formed. By the time



Text-fig. 6. *a*, larva with six chaetigerous segments, about 5½ weeks old (dorsal view); *b*, larva with nine chaetigerous segments, about 7 weeks old (dorsal view); *c*, young worm with nineteen chaetigerous segments, about 10 weeks old (dorsal view).

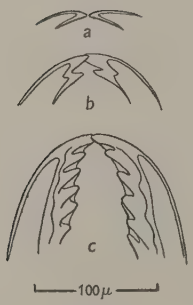
this last stage (Text-fig. 6*c*) has been reached, the young worm, which is by then between 2·5 and 3·0 mm. long, is still quite colourless, but orange pigment appears in the anterior dorsal region soon afterwards, and in the larvae with nineteen chaetigerous segments the dorsal blood vessel may be clearly seen as a deep red mid-dorsal line. By now the adult mode of life has been assumed, and the larva is virtually a miniature adult, burrowing in the mud.

Development of the Jaws and Chaetae

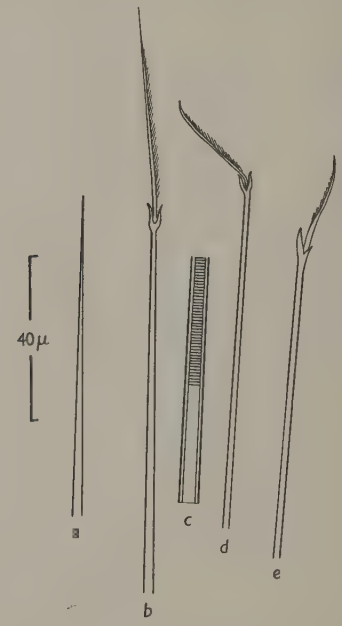
As already mentioned, jaws appear in the pharyngeal region of the larva with three chaetigerous segments. They are at first simple transparent structures and only later become toothed (Text-fig. 7). One tooth (apart from the apex of the jaw which is not considered as a 'tooth' in this description) has developed by the time the larval stage with four chaetigerous segments has been reached, and further teeth are then added until, by the time that six chaetigerous segments have been formed, five teeth are borne on each jaw. Up to this stage the jaws remain more or less transparent, and the details could be made out only in larvae fixed in benzyl alcohol. By the time that five teeth have been formed, however, the jaws are beginning to harden and assume the amber colour characteristic of those of the adult. This change corresponds with the commencement of feeding, though the buccal region does not appear to be eversible until a rather later stage. A young worm with eighteen chaetigerous segments (about 3·2 mm. long) was observed on one occasion to evert its proboscis, but this was never observed in larvae or young worms smaller than this. Paragnaths are not developed until much later.

Larval chaetae follow a succession similar in many ways to that described by Wilson (1932) in the larvae of *N. pelagica*. Homogomph spinigers predominate in both neuro- and notopodia during the early stages, with very few simple capillaries. Homogomph chaetae in *N. diversicolor* larvae have the tip turned over very slightly (Text-fig. 8). Larvae with three chaetigerous segments have, on the average, about five chaetae in each notopodium and four or five in each neuropodium. Usually there are slightly more chaetae in the notopodia than in the neuropodia. Wilson described *N. pelagica* larvae with three chaetigerous segments as having between seven and ten chaetae in each group, which is almost twice that of *N. diversicolor*. It is interesting to note in this connexion that Wilson's larvae were essentially pelagic, whereas those of *N. diversicolor* are typically bottom forms. Again, capillaries seem to be commoner in *N. pelagica* larvae than in the *N. diversicolor* larvae described in the present paper. Wilson also describes homogomph falcigers from *N. pelagica* larvae with three chaetigerous segments, but these are absent in the corresponding stage in *N. diversicolor*, though intermediate forms between homogomph spinigers and falcigers occur in slightly later larvae. All the compound chaetae have the distal parts closely toothed with long fine teeth. Heterogomph falcigers appear in later larvae, and by the time that the larva has acquired

eighteen segments heterogomph falcigers predominate in the first few segments, but in the more posterior segments homogomph bristles still remain more numerous. Young worms with thirty chaetigerous segments have a predominating number of heterogomph falcigers, but a few homogomph spinigers remain, mainly in the notopodia. This condition approaches that of the adult.



Text-fig. 7.



Text-fig. 8.

Text-fig. 7. Jaws from larvae with: *a*, three; *b*, four; *c*, six, chaetigerous segments.

Text-fig. 8. Larval chaetae. *a*, simple capillary; *b*, homogomph spiniger; *c*, fine structure of chaetae (base only); *d*, homogomph falciger; *e*, heterogomph falciger.

Apart from Wilson's close analysis of the succession of the larval bristles of *N. pelagica*, and some previous work on the same species by Herpin (1925), the development of the larval chaetae has not been closely studied. The only other detailed drawing of a larval chaeta of *N. diversicolor* known in the literature, is the drawing of a single chaeta by Hofker (1930). This author based his identification of his larvae partly on the resemblance of these chaetae to those of the adult, but it does not resemble the chaetae here described. Further, it should be noted that the larval chaetae in the very early larvae do not closely resemble those of the adult, either in character or composition.

Aciculae occur first in larvae with ten chaetigerous segments, and after this stage has been passed, develop with the chaetae as the new segments are added. The formation of the acicula is not, therefore, initiated when the parapodia attain a certain age or size after the formation of the chaetae, the two sets of structures arising concurrently after the formation of about ten chaetigerous segments. It would seem to be some function of the size or age of the larva itself, rather than that of the individual parapodium. Typical larval chaetae are shown in Text-fig. 8.

Elaboration of the Parapodia

The formation of the parapodium is of interest since its form in the adult, like that of the chaetae, is of taxonomic importance. In *N. diversicolor* the adult form is not approached by any of the parapodia until thirty or forty chaetigerous segments have been formed, and even then the older parapodia are by no means identical with those of the adult.

In very early larvae with three chaetigerous segments there are virtually no parapodia, but by the end of this stage simple notopodial and neuropodial lobes are recognizable (Text-fig. 9*a*). In larvae with four chaetigerous segments these two main lobes each begin to be divided into two main parts and the ventral cirri are plainly visible (Text-fig. 9*b*). This pattern persists over much of the strictly larval life and is much the same in larvae with ten chaetigerous segments, though the two main lobes are then much longer and supported by acicula. In a young worm with thirty-one chaetigerous segments notopodial and neuropodial lobes conform mainly to the adult plan (Text-fig. 9*e*). By this time the dorsal cirri have also appeared and the noto- and neuropodia are composed of three subsidiary lobes, which are not, however, as distinctly separated as in the adult (Text-fig. 9*f*).

It is interesting that the ventral cirrus develops first, and that the development of the dorsal cirrus is delayed until the adult life has been assumed.

For more details of the development of the parapodia reference should be made to the work of Finke (1936).

Development of the Head Region

The larva with three chaetigerous segments possesses two pairs of tentacle-like processes on the head (Text-fig. 10*a*). The anterior pair are always the shorter of the two, and represent the future prostomial tentacles. The posterior pair represent the first pair of peristomial cirri. Palps do not appear until the larva possesses four chaetigerous segments. Only one pair of peristomial cirri is present in larvae with seven chaetigerous segments, but by the time that a further two chaetigerous segments have been added, three pairs are recognizable. The full complement of four pairs is not developed till the larva

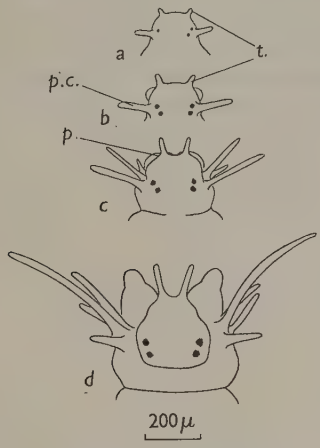
possesses about sixteen chaetigerous segments. The first two pairs of peristomial cirri are derived from the first segment, while the two pairs which are

Text-fig. 9. *a*, second parapodium of a larva with three chaetigerous segments; *b*, second parapodium of a larva with four chaetigerous segments; *c*, fourth parapodium of a larva with five chaetigerous segments; *d*, fourth parapodium of a larva with ten chaetigerous segments; *e*, tenth parapodium of a young worm with thirty-one chaetigerous segments; *f*, parapodium of adult in mid-body region. *a*, *b*, *c* and *d* are to the same scale.

added later are derived from the first larval chaetigerous segment which coalesces with the first segment to form the peristomium or 'buccal segment' of the adult (see Table III). A similar mode of development was found by

Hempelmann (1911) in *Platynereis dumerilii*, and by Herpin (1925) in other nereids.

The prostomium is not distinctly separated off by a groove until the young worm has about eighteen chaetigerous segments, when the palps are becoming elaborated into the two parts characteristic of the adult (Text-fig. 10*d*).



Text-fig. 10. Development of head region: *a*, head of young larva with three chaetigerous segments; *b*, head of larva with seven chaetigerous segments; *c*, head of larva with nine chaetigerous segments; *d*, head of larva with eighteen chaetigerous segments; *t*, prostomial tentacles; *p*, palp; *p.c.*, peristomial cirri.

Table III. Development of the Head Region

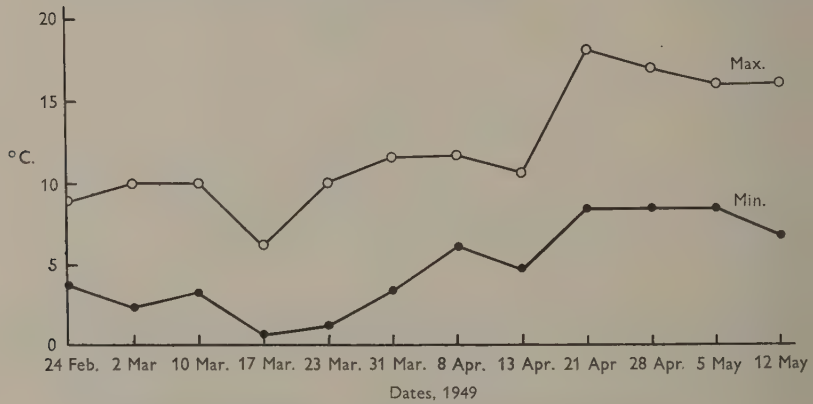
	Appendages	
	Larva with three chaetigerous segments	Larva with more than three chaetigerous segments
Prostomium	Tentacles	Tentacles
First segment	Cirri	Cirri } Peristomium ('buccal
Second segment	First chaetigerous segment	Cirri } segment')
Third segment	Second chaetigerous segment	First chaetigerous segment
Fourth segment	Third chaetigerous segment	Second chaetigerous segment

Larval Habits and Life History

The young ciliated monotrochophores are weak swimmers and never continue swimming for any length of time, frequently coming to rest on the bottom. They are somewhat denser than sea water, and in nature these swimming movements cannot be of much importance in distributing the species. Young chaetigerous larvae cannot, at first, move their chaetae, but by the end of the larval stage with three chaetigerous segments the chaetal sacs have acquired a good musculature and can be moved backwards and forwards in the

horizontal plane. By this stage, therefore, the larva can crawl on the substratum or on the walls of the parent burrow. Cilia are prominent, however, even in larvae with five or six chaetigerous segments, and in larvae with four chaetigerous segments (Text-fig. 5*c*) the prototroch and subsidiary ciliary bands are still sufficiently well developed to enable the larva to swim off the bottom. Swimming is never continued for more than a few seconds at a time, and for the most part the young larva crawls about with the aid of the anterior three pairs of parapodia which by now have acquired their own intrinsic musculature.

During swimming, the parapodia and chaetae (in larvae with three or four chaetigerous segments) are held backwards against the sides of the body so as



Text-fig. 11. Temperature of natural habitat during early larval life from time of spawning.

to reduce the water resistance. Braking is effected by the parapodia being brought forwards and extended away from the body. The first pair of parapodia are frequently directed forwards in so doing. This action of the parapodia apparently increases the water resistance of the body sufficiently to bring the larva to rest, while the cilia continue beating. This braking action also brings the parapodia into the correct position for crawling to begin again, and with fairly active larvae such crawling and swimming periods alternate.

The larvae are not, however, particularly active until about ten chaetigerous segments have been delimited. Up to this stage the larva is apparently entirely lecithotrophic, but as feeding begins at about this time (when the larva is some 7 weeks old) it is probable that this assumption of a more active life is correlated with the beginning of active feeding. Probably little distribution of larvae occurs until this time. In one instance a burrow was opened which was swarming with scores of larvae with eight and nine chaetigerous segments, and it is highly probable that these larvae resulted from a successful

fertilization in the burrow, or that the fertilized eggs had been washed into the burrow from the surface. The greatly increased activity of the larvae with ten chaetigerous segments coupled with the search for food probably serves to distribute the species, although distribution probably takes place mainly in later life.

Young worms with about twenty chaetigerous segments, and about 4 mm. in length, if placed in a deep dish with a layer of fresh mud, promptly burrow into the mud and construct minute U-shaped tubes the openings of which are only 2 or 3 mm. apart. These burrows may be seen in nature under favourable conditions.

The larvae are, therefore, typically bottom-living. Many authors, however, have ascribed larvae found in the plankton to *Nereis diversicolor* (Hofker, 1930; Smidt, 1944; Thorson, 1946), but all workers seem to be agreed that they do not really represent pelagic forms but are bottom larvae which have

TABLE IV. LARVAL LIFE HISTORY

	Lecithotrophic		Free-living larval life	Adult mode of life
No. of chaetigerous segments ...	3	10	20	
Length (mm.)	0·4	1·6	4·0	
Age (weeks)	3	7	10	
		Jaws harden		
		Colourless	Pigment appears	

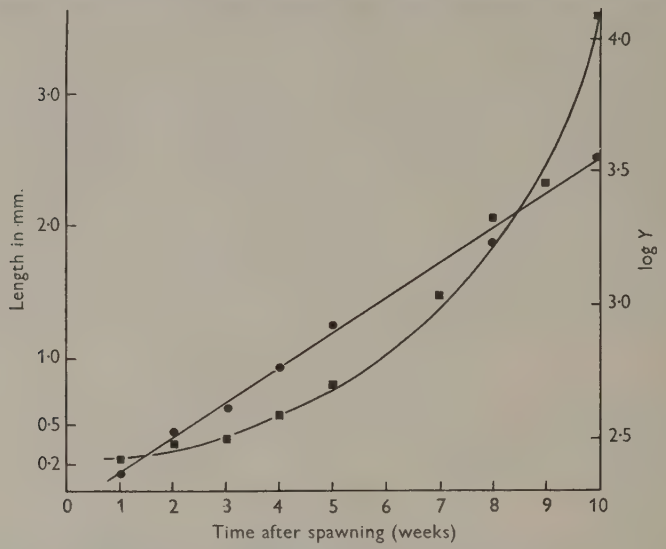
been carried up to the surface. Spärck (1926) found that young adult *N. diversicolor* appeared in cement tanks constructed during the summer in Nykøbing Mors (Limfjord) and these could only have developed from young worms or larvae swept off the bottom by currents.

The early larval life history is summarized in Table IV.

GROWTH OF THE LARVAE

Growth in the length of the larvae continued at a constant geometric rate over the early stages. The length of time elapsing between fertilization and the formation of the monotrochophore, the earliest stage collected in any appreciable numbers from the mud, was determined from the time taken for eggs in artificial fertilizations to reach this stage. The rate of growth of all the later stages was calculated from measurements of larvae obtained from the natural habitat. Collections were made every 3 days at first, and later, at weekly intervals, and all the larvae and young worms so obtained were measured. There was little size variation at first, but this became progressively greater, as would be expected, in later samples. The relative numbers of larvae in each stage were determined during the first month after the main spawning period and the frequency distributions of these samples arranged as a series of histograms in Text-fig. 2 (p. 334). Text-fig. 12 represents the rate of growth

of larvae, constructed from the mean length calculated from the measurements of several dozen larvae in each stage. The curve will be seen to follow the



Text-fig. 12. Growth of larvae during first 10 weeks.

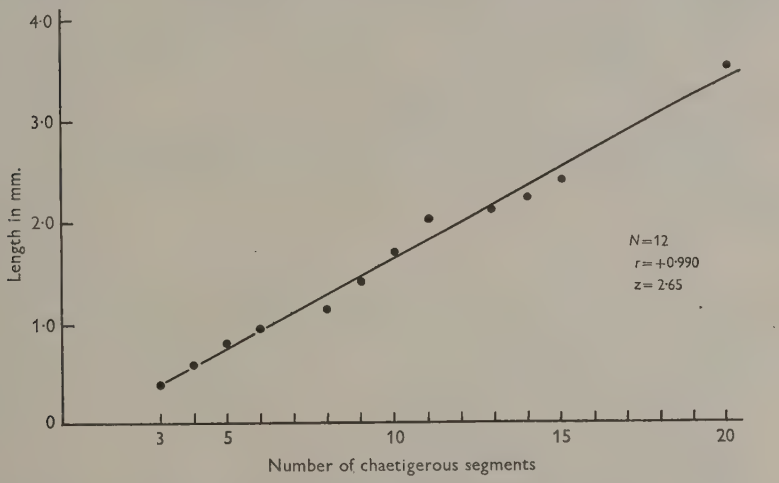
TABLE V. GROWTH OF LARVAE

No. of chaetigerous segments	Length (mm.)	Age (weeks after fertilization)
Egg to monotrochophore	0·220	1–2
Young chaetigerous larvae	0·330	2
Larvae with three chaetigerous segments	0·400	3
,, ,, four ,, ,,	0·570	4
,, ,, five ,, ,,	0·800	5
,, ,, six ,, ,,	0·950	—
,, ,, seven ,, ,,	—	6
,, ,, eight ,, ,,	1·120	—
,, ,, nine ,, ,,	1·480	7
,, ,, ten ,, ,,	1·700	—
,, ,, eleven ,, ,,	2·050	8
,, ,, twelve ,, ,,	—	—
,, ,, thirteen ,, ,,	—	—
,, ,, fourteen ,, ,,	2·300	9
,, ,, fifteen ,, ,,	—	—
,, ,, sixteen ,, ,,	—	—
,, ,, seventeen ,, ,,	—	—
,, ,, eighteen ,, ,,	—	—
,, ,, nineteen ,, ,,	3·600	10

normal logarithmic pattern characteristic of growth with a constant geometric growth rate. This growth rate (geometric, multiplicative, or instantaneous) was calculated, basing the calculations on larvae from 1 to 9 weeks in age, and

was found to be 0·04277. Details of these calculations are given in the Appendix (p. 360).

The length, age, and corresponding number of chaetigerous segments of larvae obtained from the natural habitat is summarized in Table V. During the early stages there is a nearly perfect positive correlation between the total length and number of chaetigerous segments. The graph (Text-fig. 13) shows this relation in larvae up to the age of about 10 weeks. Using the usual statistical methods (see Appendix) the calculation of the correlation coefficient '*r*' based on twelve randomly selected larvae from each size-group and having



Text-fig. 13. Correlation between larval length and number of chaetigerous segments.

between three and twenty chaetigerous segments gave a value of '*r*' as +0·9900; an almost perfect positive correlation. From this Fisher's term '*z*'=2·65. As the worms become older the degree of correlation becomes less, and in 'adult' worms the degree of correlation is too small to have any real significance.

Comparison with other Accounts of Nereid Larvae

Many species of *Nereis* are often found in the same habitat, and this has caused much confusion with regard to the identification of the larvae. Larvae found in the plankton have frequently been ascribed to *N. diversicolor*, solely on the basis that this species is the most abundant in that area. Difficulty in identifying nereid larvae is increased by their variability. Wilson (1932), for example, found certain differences between his *N. pelagica* larvae and those described by Herpin (1925); while the variation in reproduction and development of *Platynereis dumerilii* has been described by Hempelmann (1911).

A larva cannot therefore be ascribed to another species solely on the basis of slight anatomical differences from that of a known species. Conversely, under certain conditions, larvae of two species may appear remarkably similar; as for instance do Herpin's (1925) drawings of *Perinereis cultrifera* larvae and the *Nereis diversicolor* larvae described in the present paper. It would seem probable that the details of chaetae and chaetal succession would be highly specific. Although this may be so, it should be noted that the larval chaetae do not necessarily resemble those of the adult, and in the present investigation a careful study of the succession of larval chaetae did not reveal striking differences from those found by Wilson for *N. pelagica* larvae, although the larvae themselves differ appreciably in their general morphology.

Again, as already emphasized by Herpin (1925) and discussed above, there is considerable size variation in the mature oocytes of *N. diversicolor*, and consequently of the earliest larvae also.

Towards a better understanding of these problems, the larvae described in the present paper are compared with all known accounts of larvae ascribed to this species.

Comparison with Larvae Previously Ascribed to Nereis diversicolor

Some of the descriptions and drawings of larvae agree well with those here described (McIntosh, 1907, 1910; Finke, 1936); but others differ more or less widely from those described in the present paper (Schultze, 1856; Hofker, 1930; Smidt, 1944; Thorson, 1946).

McIntosh's larvae

Locality: St Andrews, Scotland.

Size: Not given (ripe oocyte given as 0·1524 mm.).

Description (1910, figs. 71–73, p. 320; fig. 74, p. 322): Chalkwell larvae correspond well with McIntosh's figures, though these are not detailed. Degree of development of head appendages and anal cirri similar in larva with three chaetigerous segments (probably an early four-chaetigerous segmented larva) and in larva with six chaetigerous segments.

Finke's larva

Locality: Kiel.

Description (fig. 1, p. 244): a larva with four chaetigerous segments closely similar to Chalkwell larvae.

Schultz'es 'larvae'

Locality: Frisches Haff; in the coelom.

Description: in no way resemble nereid larvae. Probably parasites.

Hofker's larvae

Locality: Zuidersee (plankton).

Size: small compared with Chalkwell larvae. Trochophore 140 μ (Chalkwell *diversicolor* larvae were 220 μ, and McIntosh's oocytes were little over 150 μ.)

Description (fig. 12 *a–d*, p. 200; fig. 13 *a–c*, p. 201): previously discussed by Thorson (1946). Early trochophores differ in having well-marked apical tuft; similar in having well-marked prototroch but little or no telotroch. Smaller size. Chaeta figured does not resemble Chalkwell *N. diversicolor* larval chaetae; neither do the jaws from a larva with six chaetigerous segments.

Hofker based his identification on: (1) chaetae, which he regarded as resembling the adult; (2) most abundant adult in the area. Both these points have already been discussed. Hofker's chaeta is provided with large stout teeth, never observed in *N. diversicolor* larval chaetae from Chalkwell, in which the teeth were extremely fine.

Smidt's larvae

Locality: Copenhagen Harbour (plankton).

Size: small compared with Chalkwell larvae. Larva with four chaetigerous segments less than 350 μ (Chalkwell *N. diversicolor* 600 μ). Larva with five chaetigerous segments 700 μ (Chalkwell 800 μ).

Description (fig. 5, p. 254): larvae do not resemble Chalkwell *N. diversicolor* larvae, having three eye-cups on each side. Larva with four chaetigerous segments very small; five chaetigerous segmented larva relatively larger. In larva with four chaetigerous segments prostomial tentacles and peristomial cirri apparently not developed (well developed in Chalkwell larvae) though anal cirri roughly equivalent in length. Pigment (?) on head region in larva with five chaetigerous segments not seen in Chalkwell larvae.

Thorson's larva

Locality: Øresund.

Size: smaller than Chalkwell larvae. Larva with four chaetigerous segments *c.* 450 μ (Chalkwell 550–600 μ).

Description (fig. 30, p. 67): show some resemblance to Smidt's larvae. Unlike Chalkwell larvae—parapodial lobes well developed in larva with four chaetigerous segments, anal cirri much shorter and unlike those of Chalkwell larvae, three eye-spots. Thorson's discussion of this larva, as well as that of Hofker, should be consulted.

Discussion

Many of the interesting features in the reproduction of this nereid have already been discussed. The main points of interest remaining are the alleged occurrences of the phenomena of metamorphosis, hermaphroditism, viviparity, and parthenogenesis.

Metamorphosis. Most recent authorities (McIntosh, 1907, 1910; Fauvel, 1923; Schröder, 1886; Herpin, 1925; Dehorne, 1925) agree that *N. diversicolor* is normally atoquous. Other workers (Heinen, 1911; Thieren, 1909) claim to have found epitoquous forms.

Heinen describes an epitoquous form which he regarded as *N. diversicolor*, but Herpin (1923, 1925) regards this as a confusion of species, and points out that Heinen's figures might equally well refer to *Neanthes succinea* Leuck. Heinen's drawings of the parapodia correspond fairly closely with Fauvel's drawings (1923) of *succinea*, and also the length of the peristomial cirri in Heinen's drawings resemble those of *succinea* rather than those of *diversicolor*, in which they are much shorter. Heinen, however, records the occurrence of

succinea as well, showing that he must have been aware of the similarity. Heinen regards *Nereis diversicolor* to be normally epitoquous and compares it with *N. japonica* (see Izuka, 1908). Heinen quotes Brandt and Riecke as also finding epitoquous forms at Kiel on two separate occasions.

The resemblance of the process of 'metamorphosis' described by Dehorne (1925) is only superficial, as previously pointed out by Herpin (1925). Fage (1924) and Fage & Legendre (1923) do not mention *N. diversicolor*, and the heteronereids described by Sorby (1906) were not referred to this species.

Thieren (1909), on the other hand, agrees with Heinen, and also claims to have found an epitoquous stage. Herpin regards this, as in Heinen's instances, to have been a confusion of species.

Thomas (1930*a*) found that chaetae in mature females sometimes tended to degenerate and suggested that this might be interpreted as an aborted or rudimentary step towards metamorphosis to an epitoquous condition. The significance of histolysis in relation to this problem has already been discussed.

Epitoquous forms, if they do occur, are therefore certainly rare, and it is probable that those reported are not attributable to this species. It may be concluded that *N. diversicolor* is normally atoquous. Epitoquous forms have never been found by the writer, and although a careful examination of maturing worms has been made, no anatomical changes, other than those associated with histolysis and parenchyma formation, were observed.

Hermaphroditism. Mendthal's view (1889) that the species was hermaphrodite was based on the assumption that the pear-shaped bodies which were almost certainly the dorsal ciliated organs of Goodrich (1893, 1945), were testes. He supported his argument by quoting Moquin-Tandon's discovery of an hermaphrodite nereid (*N. massiliensis*) in 1869. This is not unique, since Johnson (1908) found the minute nereid *Lycastis quadraticeps* to be hermaphrodite, while *Platynereis dumerilii* also has an hermaphrodite form (Hempelmann, 1911). Mendthal concluded that, though the worm was hermaphrodite, the male gametes ripened before the ova. Gravier (1905) considered that hermaphroditism might occur exceptionally, but McIntosh doubts Mendthal's statements, and de St Joseph also could not corroborate these views. Herpin (1923*a*, 1925) and more recent workers agree in finding the species dioecious. This is in accordance with observations made by the writer.

Viviparity. Theoretically, ovoviviparity might result from (1) parthenogenetic development of the coelomic oocytes, (2) as a result of internal fertilization, or (3) self-fertilization in the existence of hermaphroditism.

This last explanation may be discounted, although it was suggested by some of the earlier workers.

The second suggestion is also unlikely to occur, in spite of the existence of a form of sexual congress. Schröder (1886), however, thought that the sperm entered via the nephridia to cause internal fertilization, and concluded that the species was viviparous after discovering 'morulae' in the coelom, though this

observation was sceptically treated by McIntosh (1907, 1910) since Schröder failed to find the larvae later in the year. These may have been abortive cleavage stages produced by abnormal conditions, or may even have been young sperm plates. Just (1915) found in the American *N. limbata*, that the oocytes would not fertilize in the tissue juices, and this may have some significance in relation to the present problem.

Parthenogenesis. This might occur in the coelom, or after spawning. The first hypothesis has already been considered, but a further observation may be added here. The discovery by the writer of several oocytes from which the 'fertilization' membranes had become lifted off, in the coeloms of unspawned females, not only supports the theories of Heilbrunn (1924) that the elevation of this membrane is due to a purely physical effect, but also suggests that it is not therefore impossible that cleavage stages might follow, and this would then concur with the views of Smidt (1944), Thorson (1946), and the observations of Schröder (1886).

Regarding the second hypothesis, viz. that the spawned eggs may develop parthenogenetically, Herpin (1923*c*, 1925) obtained cleavage stages from the unfertilized oocytes owing to hypertonicity resulting from evaporation, or other peculiar conditions (Fischer, 1902, 1903; Dehorne, 1925; Herpin, 1925; Just, 1928*a*, *b*).

Herpin noted that the gelatinous envelopes were not always developed in these artificial fertilizations, and the writer has also found them to be frequently absent in artificially fertilized eggs, and in naturally occurring stages. Segmentation was irregular (Herpin, 1925), the cleavage stages being somewhat similar to those obtained artificially by Fischer (1902, 1903) from *N. limbata*, and to those obtained by the writer. For a general discussion of these topics reference should be made to the work by Morgan (1927).

Nereis eggs are very resistant to extreme environmental conditions, as is shown by experiments which have been performed on *N. limbata* (Just, 1928*a*, 1930*a*, *b*; Barron, 1932, etc.). The eggs of this species were found to be particularly resistant to lowered salinity and to temporary exposure to anaerobic conditions (Barron, 1932). No experiments have yet been performed on the eggs of *N. diversicolor*, though if the eggs and larvae of this species are similarly adapted to resist extreme conditions, as seems likely, then in this species this resistance may be regarded as having survival value. The relationship of breeding habits to salinity is being investigated.

Summary

An account is given of the reproduction and development of the larva of *N. diversicolor* O. F. Müller.

In any one population the number of males was found not to exceed 10 %.

The species is dioecious. Both sexes become green at maturity, but may be distinguished externally.

Ripe oocytes, which vary between 200 and 250μ in diameter mature in a loose coelomic parenchyma, and are released by rupture of the body wall after its partial histolysis. Sperm is released through the nephridia, or possibly by rupture of the body wall as well. In the male histolysis occurs, but the coelomic parenchyma is transitory. Sperm matures in the form of coelomic sperm plates.

Spawning was found to take place over a limited period centred in 1949 round the third lunar quarter in February after a sharp rise in temperature. Spawning has been found to take place generally in early spring; variations are discussed. A form of sexual congress occurs.

Larvae develop in the mud, and there is no true pelagic phase.

Development is relatively slow. Cilia are not well developed in the larvae. The external morphology of the larva is discussed.

The young larvae become active when 7 weeks old, and the adult mode of life is assumed at 10 weeks, when the worm is 4 mm. in length.

The species is atoquous.

Parthenogenesis, hermaphroditism, and viviparity do not normally occur.

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APPENDIX

Table VI. Growth of Larvae

Calculation of the geometric growth rate, based on larvae 0 and 9 weeks after hatching, using the equation

$$G=\frac{\log Y_t-\log Y_0}{0{\cdot}4343t},$$

where Y_0 = length of larvae 0 week after hatching, Y_t = length of larvae 9 weeks (63 days) after hatching, $t=63$ days. Then

$$G=\frac{3{\cdot}54-2{\cdot}37}{(0{\cdot}4343)\,63}=0{\cdot}04277.$$

Table VII. Growth of *Nereis diversicolor* larvae

Correlation of length and number of chaetigerous segments.

Calculation of the correlation coefficient 'r'

No. of chaetigerous segments (X)	Length (mm.) (Y)	d_X	d_Y	d_Xd_Y	d_X^2	d_Y^2
3	0·40	−6·83	−1·21	8·260	46·650	1·464
4	0·57	−5·83	−1·04	6·063	33·990	1·082
5	0·80	−4·83	−0·81	3·912	23·330	0·656
6	0·95	−3·83	−0·66	2·527	14·670	0·436
8	1·12	−1·83	−0·49	0·897	3·350	0·240
9	1·40	−0·83	−0·21	0·174	0·688	0·044
10	1·70	+0·17	+0·11	0·018	0·289	0·012
11	2·05	+1·17	+0·44	0·515	1·369	0·194
13	2·10	+3·17	+0·49	1·553	10·050	0·240
14	2·20	+4·17	+0·59	2·460	17·390	0·348
15	2·40	+5·17	+0·79	4·084	26·730	0·624
20	3·60	+10·17	+1·99	20·230	103·500	3·960
Σ 118	19·29	—	—	50·693	282·006	9·300

Also

$N=12$, $M_X=9{\cdot}83$, $M_Y=1{\cdot}61$; and from above

$\Sigma d_Xd_Y=50{\cdot}693$, $\Sigma d_X^2=282{\cdot}006$, $\Sigma d_Y^2=9{\cdot}300$.

Using the equation

$$r=\frac{\Sigma d_Xd_Y}{\sqrt{(\Sigma d_X^2\,\Sigma d_Y^2)}},$$

$$r=\frac{50{\cdot}693}{\sqrt{(282{\cdot}006\times 9{\cdot}300)}}=+0{\cdot}9900$$

From this, Fisher's term 'z'$=2{\cdot}65$.

EXPLANATION OF PLATE I

Fig. 1. Transverse section of an almost mature female showing oocytes in the coelom and parapodial spaces. × 30.

Fig. 2. Sperm plates in the coelom of an immature male. × 120.

Fig. 3. Early stage in the growth of the oocytes: beginning of parenchyma formation. × 120.

Fig. 4. Later stage in the growth of the oocytes: coelom filled with parenchyma. × 120.

Fig. 5. Ripe oocytes: parenchyma breaking down into discrete cells. × 120.

Fig. 6. Living larva with four chaetigerous segments. × 100.

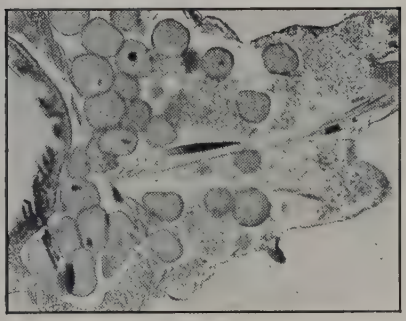


Fig. 1.

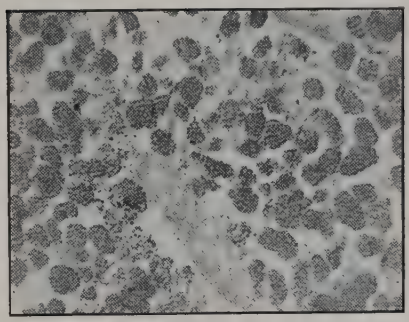


Fig. 2.

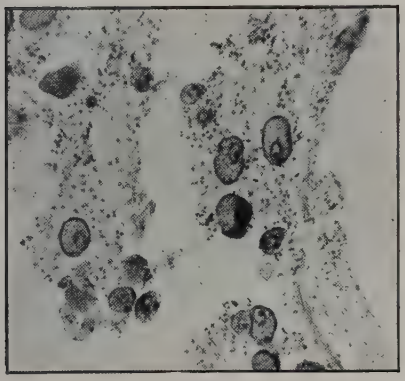
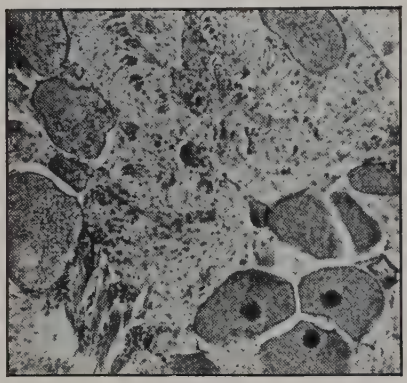


Fig. 3.



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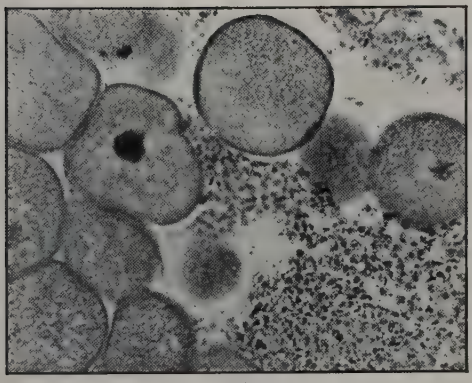


Fig. 5.

Fig. 6.

THE DISTRIBUTION OF *OCTOPUS VULGARIS* LAMARCK IN BRITISH WATERS

By W. J. Rees, D.Sc.

British Museum (Natural History)

(With Plates I–III and Text-figs. 1–3)

CONTENTS

	PAGE
Introduction	361
The distribution of *Octopus vulgaris*	362
The English side of the Channel	362
The Channel Islands and the north coast of France	363
The southern North Sea	364
Other British coasts	364
A brief review of early development	366
The Channel larvae	368
Stations at which larvae were found	368
The identity of the larvae	370
Description of the larvae	370
The source of the *Octopus* population in British waters	372
The rarity of spawn and larvae in inshore waters	372
The dispersal of larvae by water movements	373
The plague years	374
Summary	376
References	376

Introduction

Octopus vulgaris Lamarck is usually regarded as a Lusitanian member of our fauna. It is found on the south coast of England, and, as E. J. Allen noted (Marine Biol. Assoc., 1931, p. 278) 'generally only a few specimens are taken during the summer months, but it varies greatly in abundance in different years'. In 1899–1900 there was a great plague of *Octopus* all along the south coast of Devon and Cornwall, which served to accentuate the rarity of the species in other years. This phenomenon was the subject of a report by Garstang (1900). Another puzzling feature was the paucity of records of *Octopus* larvae and spawn in our inshore waters which at once suggested that the species rarely breeds on the English coast. If so, how was the population maintained from year to year and whence did the larvae or adults come? During the recent cruises of the M.Y. *Manihine* planktonic larvae of *O. vulgaris* have been found for the first time in fairly substantial numbers in the Channel. These yield much information on the early larval *Octopus*, and also I believe on its distribution in the Channel and southern North Sea.

In order to present as complete a picture as possible, I have thought it desirable to review earlier records for the south coast of England, the Channel Islands and the French coast, the southern North Sea and other British records.

Acknowledgements are due to Major H. W. Hall, M.C., whose interest in marine biology led to the very generous loan of the M.Y. *Manihine* for this and other investigations in the English Channel.

I am also especially indebted to Dr H. W. Parker for facilitating my work in various ways. I wish to thank: Mr D. W. Tucker for the care he took in the preservation of some of the larvae, Dr D. P. Wilson for the use of the photograph on Plate I, and Mr G. L. Wilkins for his admirable drawings. My thanks are also due to Mr H. O. Ricketts and Miss B. Skramovsky for technical assistance.

The Distribution of *Octopus vulgaris*

O. vulgaris has a wide distribution in the warmer waters of the Atlantic. It is found from the English Channel southwards as far as the Cape of Good Hope, in the Mediterranean, the Caribbean, at the Canaries, the Azores and Bermuda (Robson, 1929; Pickford, 1945). Farther afield it occurs at some places in the Indian Ocean and in Japanese waters (Sasaki, 1929). It is the common octopus of the Mediterranean where it is the object of fisheries at many places. It has been reported on many occasions from the Red Sea.

The English Side of the Channel

The species occurs in inshore waters along the whole of the south coast from Land's End to Dover, but except in some years it is seldom common. According to Forbes & Hanley (1853, p. 210) the first British record was from Dover; later in 1841 it was taken at Plymouth by Robert Ball. Lee (1875) mentions a specimen captured in a lobster pot at Eastbourne, one from Mevagissey and another from Brighton; all these were exhibited at the Brighton Aquarium in the days when *Octopus* was a star attraction. Other sporadic records indicate that the species is found along the whole coast.

In the years 1899–1900, as mentioned above, there was a plague of *Octopus* along the south coast of Devon and Cornwall. According to Garstang (1900), *Octopus*, which had been scarce in the neighbourhood of Plymouth since the opening of the Laboratory there, became more plentiful from January 1899 onwards. During 1900 the increase reached the dimensions of a plague which had a disastrous effect on the crab and lobster fisheries along the whole coast of Devon and Cornwall. Not only did the *Octopus* invade the crab pots, but they were so numerous, in September 1900, as to drive large crabs out of their normal haunts below low-water mark on to the intertidal region in Plymouth Sound. In the same year Allen & Todd found several *Octopus* 'nested' on the shore of Salcombe Estuary, and Garstang records a minute

Octopus larva in a tow-netting in the same estuary in August. Garstang was inclined to attribute the startling increase of *Octopus* to the warm summers and the mild winters experienced from 1893 onwards, these providing favourable conditions for a warm-water animal. This view is discussed in relation to distribution problems below (p. 374).

Minor plagues appear to have occurred at Brighton in 1913 and 1922 (Robson, 1929), and in the summer of 1948.

Lee (1875, p. 64) records an *Octopus* with its spawn taken in a dredge off Brighton in March 1874. Apart from occasional spawning under artificial conditions in public aquaria, and the two records mentioned, I can find no other records of spawning or of larvae in our inshore waters. Crawshay (1912), in his thorough report on the fauna of the Outer Eddystone, and F. S. Russell, in numerous plankton reports from the Plymouth area, mention neither spawn nor larvae.

Another interesting feature of *Octopus* distribution on the English coast is the absence of nested specimens at low water on the shore, except in plague years.

The Channel Islands and the North Coast of France

Octopus is fairly common on the shore at low water in the Channel Islands and has been reported on numerous occasions.

Dautzenberg & Fischer (1925, p. 1) state that the species is common on both west and north coasts of Finistère. In the Bay of St Malo, Dautzenberg & Durouchoux (1913, p. 7) record its occurrence in shallow water in the *Zostera* beds or lurking under large stones or in crevices of rocks, presumably on the shore. They say that its presence when nested is often indicated by masses of bivalve shells of molluscs on which it feeds.[1]

On the Normandy coast it is recorded for the north and east coasts of the Cherbourg peninsula by Kerville (1898, 1901). He found small specimens on the shore between tide marks on the beach at St Martin, to the west of Omonville la Rogue, as well as specimens in lobster pots. In this area the species is regarded as more or less common. On the east coast of the peninsula, Kerville states that it is very common in holes in rocks and under large stones in the region of Grandcamp-les-Bains. A large specimen was caught between tide marks on the Îles Saint-Marcouf.

Still further east, Loe & Raeymaekers (1885, p. 212) record *Octopus* from the Bay of the Somme, where it is sometimes thrown up on the beach after storms and frequently taken by fishermen in their nets.

Giard (1885, p. 302) also mentions *Octopus* in the eastern end of the Channel from Tour de Croy and Pointe à Zoie, Audresselles. It appears that it is very common under stones from April to September.

The plague year 1899, in particular, is mentioned by Kerville (1901). The

[1] Mr A. E. Salisbury informs me that in the Channel Islands these remains consist almost entirely of *Paphia rhomboides* (Pennant).

species was then very abundant in the region of Omonville la Rogue. Dautzenberg & Fischer (1925) also mention for Finistère that the species was very abundant in some years. Garstang gives additional information, derived mainly from newspaper reports, about the plague on the French coast in which *Octopus* appears to have been as abundant in 1899 as in 1900—unlike the situation on the English coast where the peak as regards numbers was reached in 1900. It appears that the infestation, if it may be so termed, affected the whole coast of Finistère and the Channel Islands, and extended eastwards at least as far as Omonville la Rogue. As on the English coast the lobster and crab fisheries were ruined for the time.[1]

Two features emerge from this survey. The species is normally found close inshore, even nesting at low water on the shore, a habit which occurred on the English coast during 1900. The abundance of *Octopus* reached the dimensions of a plague about a year earlier than it reached its peak on the English side. The significance of these points is discussed below (p. 375).

The Southern North Sea

Records of *Octopus* in the southern North Sea are few and the species appears to be rare. Robson (1929) mentions a specimen from the River Crouch, Essex: this is the only record that can be verified from the east coast of England. For the Belgian coast Adam (1933) has shown that many of the older records are not reliable, but quotes an early record by van Beneden (1883). Adam reported a specimen from Ostende and another taken between Blankenberghe and Orfordness. As Adam remarks, the capture of only two specimens during an intensive survey of the southern North Sea, between 50 and 53° N., is an indication of the rarity of the species in the area.

Tesch (1908), mainly quoting earlier records, mentions several specimens from the Dutch coast, but some of these need verifying. Only three specimens are known from the German coast. One, labelled 'Westerems (Rottum)', is in the Leipzig Museum, and another in the Berlin Museum is from Heligoland. The third was reported from the Borkum area by Hertling (1936).

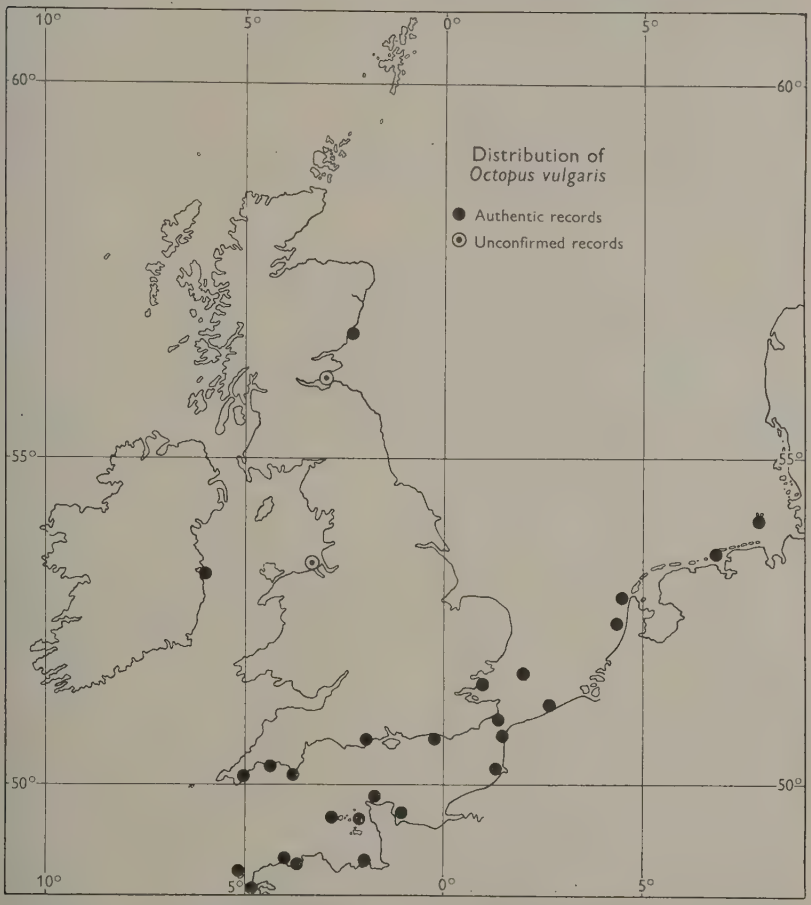
There are no records from the Danish, Swedish and Norwegian coasts.

Other British Coasts

Records of *Octopus* from other British coasts are few and most of them have been discounted by Grimpe (1925) and Robson (1929). The species has been confused with *Eledone cirrosa* which normally has a single row of suckers on

[1] Since this part of the paper was written, I have been privileged to examine a file of newspaper cuttings kept by Mr R. Winckworth. It appears that there was a plague of *Octopus* on the coast of Finistère in 1922 with the usual disastrous effect on the shell-fisheries (*The Times*, 27 March 1922). According to one report the crabs were seeking refuge on the shore in July of that year (*Daily Mail*, 11 August 1922).

each arm. In the latter the suckers may appear to be biserial, as in *Octopus*, particularly in contracted specimens. Occasionally an abnormal *Eledone* is found in which the suckers are irregularly biserial (Gravely, 1908).



Text-fig. 1. The distribution of *O. vulgaris* in North European waters. Token records only are given for the English Channel but all records (usually referring to one or two specimens each) are plotted for other areas.

Early records from the Firth of Forth cannot be verified, but Stephen (1937) confirms a record of a very juvenile specimen, of 1·5 cm. in mantle length, picked up on the beach at Montrose in 1893.

Nearly all of the old Irish records are also doubtful, but the specimens reported by Haddon (1886) from Dublin Bay are in the Museum of Trinity

College, Dublin. These were re-examined by Massy (1909, p. 6), who confirmed that they were *Octopus vulgaris*.

Darbisher (1886, p. 245), in his report on the molluscan fauna of the L.M.B.C. district, mentions a large female *O. vulgaris*, taken in the Albert Dock at Liverpool, in September 1854 by T. J. Moore. The specimen appears to have been lost, as Hoyle (1886), who examined the remainder of the Liverpool Bay Cephalopoda, omits all references to it. This can only be regarded as an unconfirmed report.

The above are the only records which I have been able to find for the remainder of the British coasts. They indicate that *O. vulgaris* is extremely rare except in the Channel.

A Brief Review of Early Development

The courtship and mating of octopods has been described for several species: Racovitza (1894) gives a good account of the present species.

The eggs (Pl. I) are laid in festoons attached to rocks or stones, and, as noted by Robson (1929), there is a well-marked tendency to deposit them in dead shells of other molluscs or in other suitable cavities. The 'nesting' or lair-building habit of the Common Octopus was thought to be an essential part of the spawning, but Heldt (1948) has shown that the laying of batches of eggs may take place without any nidification as a preliminary.

The eggs, described by Naef (1928), Heldt (1948) and Pickford (1950), are small with an oval capsule about $2{\cdot}5 \times 1$ mm. and the stalk is more or less as long as the capsule. A characteristic feature, which has recently been given prominence by Pickford, is the small oval swelling on the stalk; this should serve as a useful means of separating the species from other octopods.

The eggs of *Eledone cirrosa* differ greatly from those of *Octopus*, with which there need be no confusion. The former are pear-shaped with a short stalk and are much larger (*c.* $7 \times 2{\cdot}5$ mm.).[1] Gravely (1908, Pl. II, figs. 7, 8) gives good illustrations.

Heldt gives the first reasonably accurate estimate of the number of eggs produced by an *Octopus* (in an aquarium tank at Salammbô, Tunis). The *Octopus* laid 192 festoons, which, if laid end to end, would have formed a string 11·5 m. long. Madame Heldt estimated that there was a total of 150,000 eggs.

At Naples, Lo Bianco (1909, p. 654) records that spawning in the aquarium takes place from May to September, and Heldt mentions October as the time of spawning of her specimen. Tandy's eggs from Florida were found in August, and Pickford (1950) mentions eggs laid in March and August from the same locality. In the Channel, as already stated, Lee (1875) records an *Octopus*

[1] Naef (1928) gives 6–9 mm. as the length of *Eledone* eggs.

with its eggs in March 1874, while Garstang's larva from Salcombe was found in August and must have come from eggs laid not later than June or July. Portmann (1933), working at Banyuls, found eggs in various phases of development and concluded that they had been developing for about 8 days. They hatched on 4 September, about 18 days after spawning. On the other hand, Naef (1928), working at Naples, found that the larva took 28 days to develop. Portmann attributed the rapid development of his larvae to the high temperature of his aquarium (24–25° C.). In view of much lower temperatures in the Channel, development there may be expected to take at least a month, possibly even longer, and in breeding areas larvae are probably hatched from April or May until the end of September.

According to Lee (1875): 'At this early stage of its existence the young *Octopus* seeks and enjoys the light.' But Portmann states that in his larvae phototropism was less marked than in *Loligo*. This author admits a great mortality among the developing eggs, but assumes it to be due to the absence of the parent, and to the inadequate aeration of some of the eggs.

The early development of the larva within the egg has often been studied. Naef (1928) and Portmann (1933) sum up our knowledge of this development, and the latter states that the fully developed larva possesses a small external vitelline sac at its birth, its contents being absorbed soon after, or sometimes even before, hatching.

Even before hatching the minute *Octopus* is provided with numerous groups of small bristles (Köllikersche Bundel), scattered over the whole outer surface, and Naef considers that their function is to assist the larva to leave the egg. He states: 'These spines or bristles are used when the egg hatches, as seen by me in *Octopus vulgaris*. The hatching occurs with the posterior end in front, as is usual in dibranchiate cephalopods, the opening is rather small, and is situated on the thicker end of the egg capsule; the exit is the same place through which the spermatophores entered, that is, the micropyle. Through this small opening the animal has to liberate itself, this process being helped by the spines which act as hooks. Sometimes the embryo is wrongly placed in the egg capsule, that is, with the oral end towards the opening, in which case it becomes impossible for it to leave the egg capsule and it dies, as it is impossible for it to turn round inside the egg and the spines are now directed in such a way as to face the opening, and so prevent the animal from leaving the capsule.' Portmann disputes these conclusions and points out that in some larvae (7 hr. after liberation) the bundles were still hidden beneath the skin. Querner (1926), on the other hand, considers that these structures indicate that the ancestors of cephalopods were provided with bristles similar to those of annelids. Whatever purpose these bristles serve during liberation, it appears that they help to keep the animal afloat and later develop into the warts which are so characteristic of the skin of the *Octopus*.

The post-embryonic life of the larva has been little studied. Naef (1923,

text-figs. 400, 409) gives a thumb-nail sketch of the newly emerged *Octopus*, of about 1·5 mm. in ventral mantle length, and of some slightly older larvae of about 1·8 mm. in ventral mantle length. He records that larvae of this size are fairly common in the plankton in the Gulf of Naples during the summer and autumn. Naef further remarks that older juvenile stages are not found in the plankton and assumes that they settle on the sea floor, undergoing metamorphosis buried in the sand or detritus, and are found again when they are much larger and have assumed the shape of the adult.

The Channel Larvae

Naef's view of a very brief plankton stage in the life of an *Octopus* has been generally accepted for this species, and Portmann, for example, remarks: 'Il se peut donc que la vie d'*Octopus* ne comprenne pas une première étape pélagique et que la larve mène déjà la vie de la pieuvre adulte.' It was therefore quite unexpected that *Octopus* larvae should be found in the plankton in the middle of the Channel and that they should still be planktonic at a much larger size than mentioned by Naef.

Octopus larvae were found at the stations enumerated below. These are shown in the map in Text-fig. 2 as black circles.

Stations at which Larvae were Found

St. 47. 31. viii. 48. 49° 55′ 20″ N., 02° 08′ W. Sounding 109 m.; N 100 B, 90–0 m. Four larvae.

St. 48. 31. viii. 48. 49° 52′ 10″ N., 02° 10′ 10″ W. Sounding 78 m.; N 100 B, 73–0 m. Seven larvae.

St. 49. 31. viii. 48. 49° 50′ N., 02° 08′ 45″ W. Sounding 73 m.; N 100 B, 69–0 m. Five larvae.

St. 50. 31. viii. 48. 49° 49′ N., 02° 28′ 45″ W. Sounding 127 m.; N 100 B, 100–0 m. Four larvae.

St. 51. 31. viii. 48. 49° 50′ 20″ N., 02° 31′ 40″ W. Sounding 155 m.; N 100 B, 93–0 m. Four larvae.

St. 60. 20. viii. 49. 50° N., 1° 54′ W. Sounding 75 m.; N 100 B, 46–0 m. Seven larvae.

St. 61. 21. viii. 49. 50° 04′ N., 1° 57′ W. Sounding 60 m.; N 100 B, 46–0 m. Thirteen larvae.

St. 62. 21. viii. 49. 50° 06′ 30″ N., 1° 49′ 30″. W. Sounding 57 m.; N 100 B, 43–0 m. Ten larvae.

St. 63. 21. viii. 49. 50° 10′ 30″ N., 1° 55′ W. Sounding 55 m.; N 100 B, 53–0 m. Two larvae.

St. 64. 21. viii. 49. 50° 12′ 30″ N., 1° 47′ 30″ W. Sounding 55 m.; N 100 B, 51–0 m. One larva.

St. 71. 30. viii. 49. 49° 58′ 0″ N., 2° 48′ 30″ W. Sounding 66 m.; N 100 B, 29–0 m. Three larvae.

St. 72. 30. viii. 49. 49° 47′ N., 2° 42′ 20″ W. Sounding 124 m.; N. 100 B, 56–0 m. Seven larvae.

St. 73. 30. viii. 49. 49° 37′ N., 2° 30′ 30″ W. Sounding 64 m.; N 100 B, 26–0 m. Two larvae.

Text-fig. 2. The distribution of *Octopus* larvae (black circles) as found during the cruises of the M.Y. *Manihine* in the Channel during the summers of 1948 and 1949. Negative stations (open circles) are also plotted to show the areas worked during the investigations.

The Identity of the Larvae

Naef could be certain only about the identity of his first stage, which he obtained from the egg, and attributed his planktonic larvae to *O. vulgaris* because of their similarity to the first stage. The youngest larvae from the Channel agree in every particular, as regards chromatophore pattern and other details of external form, with Naef's description. Quite apart from Naef's work, it would have been possible to refer the Channel larvae to *O. vulgaris*. No other octopod with biserial suckers occurs in the Channel, and this arrangement is just discernible even in the youngest larvae, and is quite distinct in the older larvae. I have therefore no doubt that the larval series from the above stations belong to *O. vulgaris*.

Description of the Larvae

As we would expect, the larvae, in common with other Octopodinae with small eggs, are quite unlike the adult and exhibit several characteristics.

There is a distinctive type of larval coloration consisting of large, prominent, reddish brown chromatophores arranged in definite patterns. On the arms, there is at first a single row, and on the dorsal side of the head a symmetrical arrangement, which is fairly constant in all the younger stages. The junction of mantle with the dorsal side of the head is clearly visible, and just behind this junction there are usually two orange-coloured chromatophores; these are situated laterally (i.e. latero-dorsal), but sometimes they are faint and apt to be overlooked in preserved specimens. Near the posterior end of the body, also situated latero-dorsally, there are two reddish brown chromatophores and sometimes additional ones (to be mentioned later). The ventral surface of the mantle and the posterior end carries about twenty distinct reddish brown chromatophores; these form a more or less definite pattern, but its irregularity in preserved specimens appears to be caused by contraction of the mantle. Those nearest to the margin of the ventral mantle are usually in a row of six.

The funnel carries four chromatophores, all ventral, two near the tip and two near the base; the latter are usually concealed by the mantle margin. There is a pair of very large chromatophores on the ventral head, one on either side or slightly covered by the lateral margins of the funnel, and there is also an extra large chromatophore at the base of each ventral arm.

There is a prominent group of large reddish chromatophores, six to ten in number, inside the mantle on the dorsal surface of the viscera; these can be distinctly observed through the mantle. In the earliest stages there are no chromatophores on the face of the arms. As the larva grows, additional chromatophores, which are described later, begin to appear.

The eyes are large, sunken in the head, and are covered with dark brown pigment. To the outside of this pigment there are numerous iridocytes, which give parts of the eye a bluish-green metallic sheen.

The arms are quite short in early stages (Pl. II, figs. 1, 2). They are all about the same length and have a thin whip-like terminal portion.

The youngest Channel larvae were provided with three or four primary uniserial suckers, each with a diameter of 0·175–0·2 mm. Larvae of 2·25–3·45 mm. (mantle length) had primary suckers of 0·25–0·3 mm. in diameter. In larger larvae of 3·75–6·0 mm. the diameter of primary suckers reached 0·35–0·55 mm. and those of the first part of biserial suckers, 0·25–0·5 mm.

The web is poorly developed, showing no sign of differentiation in depth. Only the rims of the jaws appear to be chitinized.

The newly hatched *Octopus* is covered on head, mantle and arms with numerous groups of bristles; but in the preserved specimens the latter are not easily seen, because they tend to disappear in formalin. They are believed, apart from whatever role they may play in the release of the larvae from the egg, to have some significance in the planktonic life of the animal (Naef, 1928; Adam, 1937). In the Channel larvae they are present at all stages up to the largest of 6 mm. in ventral mantle-length. In the latter, they appear to be in process of being transformed into the warts of the adult.

In the youngest larvae the mantle width is frequently greater than the mantle length. Between 1·8 and 2·4 mm. (that is, in ventral mantle length) the length overtakes the width, and beyond this size the mantle length is always greater than the width. This is clearly indicated in Text-fig. 3, where the mantle width is expressed as a percentage of the mantle length. There is a suggestion too that the mantle is more elongated during its growth between 3 and 4·5 mm. than when it grows beyond this stage. Unfortunately the number of larvae of this size are too few to give adequate results and it must be remembered that the mantle itself is capable of much variation.[1]

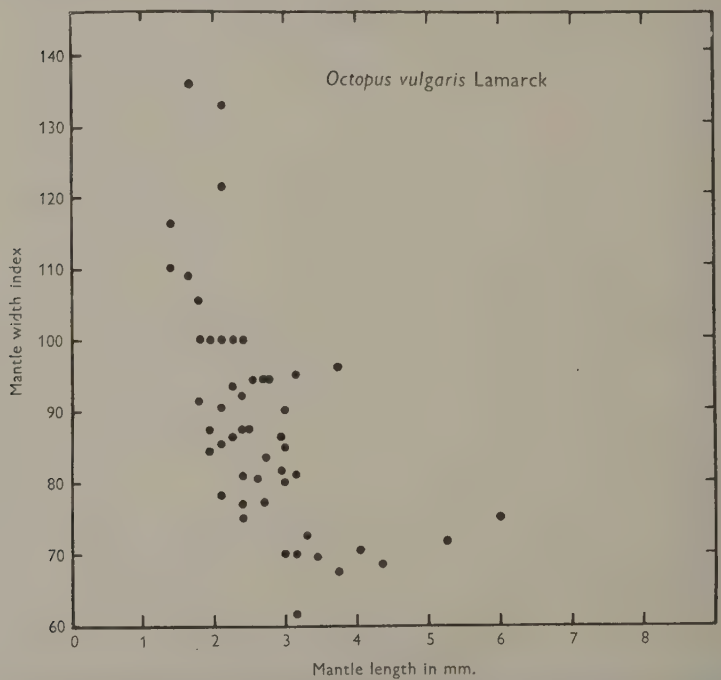
The following brief description applies to the largest larva found (Pl. III). This specimen has already acquired many adult characters, such as the proportions of the mantle and head, but the arms are still quite short. These are subequal, and in the contracted state are about 7 mm. long. The web, too, is subequal and reaches as far as the first row of double suckers. On the oral face of the arms there are no chromatophores on the suckers in the proximal web region, but reddish brown ones occur between the biserial suckers beginning with the first pair (Pl. III, fig. 8). Some suckers on the arms are also developing chromatophores around their rim, in the same way as illustrated by Adam (1937, fig. 30 H) for his *Octopus* larva from the coast of Brazil.

The outer surfaces of the arms carry a double row of evenly spaced chromatophores, and, in addition to these, two further rows are developing, one on either side of the arms; those on the dorsal and dorso-lateral arms are

[1] The ventral mantle length is used by all workers on Cephalopoda and is regarded as a more reliable measurement than those of the head, arms and funnel. It is for this reason that I have refrained from giving measurements of the head and arms, but the proportions in larvae at different stages can be seen from the drawings.

better developed than those on the ventral arms. There are also light orange-coloured chromatophores developing in the surface skin of the head and web. Some on the former are difficult to see because they are situated over the more deep-seated chromatophores of the head region. In this specimen there are also four reddish brown surface chromatophores on the surface of the mantle, at its junction with the head.

Intermediate younger stages are illustrated in Pl. I.



Text-fig. 3. The relation of mantle length to mantle width in the Channel larvae. The mantle width is expressed as a percentage of the mantle length.

The Source of the *Octopus* Population in British Waters

The Rarity of Spawn and Larvae in Inshore Waters

It has already been indicated that the eggs of *Octopus* have been found only on one occasion on our coast. This alone is insufficient proof of absence of regular breeding, because the eggs of *Eledone* are almost equally scarce and both species probably lay their eggs in places which are almost inaccessible to the ordinary dredge or trawl. The absence of any report of planktonic larvae,

except in the abnormal year 1900, during the whole existence of the Plymouth Laboratory is much more significant and may be regarded as reasonable proof that the species breeds here only under abnormal conditions. *Eledone*, as is well known, breeds all round our coast but its larvae are rarely found in the plankton for a very different reason, so I believe. Its eggs are large, 6–9 mm. in length, so that the embryo is able to complete its larval development before hatching. As Naef (1923) has shown, the young *Eledone* already possesses all the characteristics of the adult form, and so on liberation is nearly ready to settle down to a benthic existence.

It is therefore extremely doubtful whether the *Octopus* is able to maintain a breeding stock on the English side of the Channel, and the most likely explanation is that the population is an immigrant one, maintained each year by an influx of young from the south, reinforced in exceptional years by limited local breeding.

The Dispersal of Larvae by Water Movements

The duration of the planktonic life of the young *Octopus* is certainly not short as assumed by Naef. Judging from my larvae the period could not be less than 1 month and might even be 3 months, under exceptional circumstances. This moderately long planktonic life enables us to consider dispersal by currents and other water movements. In this connexion, the work of Carruthers (1927) with drift bottles in the English Channel proves very interesting, especially as many of his bottles were released in approximately the area in which the larvae were found. Most of the larvae appear to have been taken in the mid-water and surface layers with open nets.

Although the larvae are not strictly comparable to either surface or bottom bottles, the experiments of Carruthers are of sufficient interest to indicate in a broad way the future movements of larvae. I have not considered the movements of surface bottles very closely, because they may have been unduly influenced by wind drift, and the bottom bottles are probably more reliable for our purpose.

There is an easterly set along the north coast of Finistère which impinges on the Manche coast and swings northwards past the Channel Islands. This is borne out by both surface and bottom bottles. To the north of the Channel Islands, as Carruthers states, 'there seems to be in longitude 2° W. (approximately) a parting of the ways in respect of the movements of the bottom water. To the north of 50° N. latitude there appears to be a west-going bottom set, whereas south of this parallel there is a set going in an easterly direction'. This is the very area in which the *Octopus* larvae occur; many of the latter are obviously recently hatched, some being no longer in mantle length than specimens just released from the egg. The hydrographic conditions indicate that they come from the south, that is, the Channel Islands, the Manche coast, and possibly also the north coast of Finistère. These areas are undoubtedly

important, if not the main, breeding grounds of *Octopus* in the Channel, and from them the species is distributed westwards to Lyme Bay and beyond, and eastwards to Dover and also occasionally into the North Sea. It is also possible that Lyme Bay may draw some of its *Octopus* from a more south-westerly source, as may Cornwall and the Plymouth area. We do not know whether *Octopus* reaches Cornwall from the east in 'Channel water', or from across the Channel, in one of the bodies of water known to penetrate into the Channel occasionally from Ushant and the Biscay region (see Russell, 1939). As far as I am aware, no larvae have been taken in this outer part of the Channel, and it may be that they become benthic at some distance from our coast. Winckworth (1928), discussing the scarcity of male specimens, states 'the scanty evidence available points to the probability that mating takes place in deeper water after which the females migrate towards the shore to spawn'.

There may also be subsidiary breeding areas along the French coast between the Cherbourg Peninsula and Boulogne, but available evidence indicates that *Octopus* is much less abundant there than it is to the west of the Peninsula.

The conditions found by Carruthers (1927) were those existing in July 1924, and as Russell has shown (1939) the water circulation in the Channel is very variable. These fluctuations will regulate the number of larvae distributed to various points of our coastal areas, so that Brighton, for instance, may have a dearth of *Octopus* during a year when they are fairly common in Lyme Bay.

I am inclined to regard the easterly set along the north coast of Finistère, carrying larvae to the coast of the Manche and the Channel Islands, as a very important factor in maintaining the stock of *Octopus* in the Channel, as the larvae would reinforce the local stock at this northern limit for breeding. As temperature is undoubtedly the most important factor controlling breeding in this area, a succession of years of low sea temperature would mean that few larvae would hatch out and reach maturity. These reinforcements would help to maintain the stocks.

The Plague Years

The plague years 1899 and 1900 were probably due to a combination of factors, all favourable to the multiplication and spread of the species in the Channel.

As already mentioned, temperature is undoubtedly a controlling factor and, as Garstang believed, the abnormal conditions probably began in 1893, an exceptional year, during which 'Under the influence of the great heat the temperature of the Channel waters rose continuously until in August it had attained a point unprecedented for a quarter of a century.... In June the tow-nets were crowded with Salps, while towards the latter end of August they were almost choked by masses of living Radiolaria.... Even the bottom fauna was influenced, as was shown by the extraordinary abundance in the Sound....'

(Garstang, 1894). The French coast, too, was influenced by the exceptional conditions, as there was a heavy fall of oyster spat in that year (Herdman, 1893). Later (1900) Garstang adds: 'The warm summers and mild winters which we have experienced during the past few years (i.e. since 1893) have also provided the conditions most suitable to a warm water animal and have favoured its residence in our inshore waters.'

The fauna of the north-west coast of France and the Channel Islands is much richer in southern species than the corresponding coast of Britain. This may be partly accounted for by a slightly higher temperature, but the hydrographic conditions undoubtedly play a big part. Unfortunately, we know so little about the penetration of various bodies of water, from the mouth of the Channel and the Biscay area, along the south side of the Channel. The relative abundance of the commoner littoral forms on the two sides of the Channel, has been the subject of a report by Fischer-Piette (1936).

On the French side of the Channel there appears to have been a gradual building up of stocks during these years, culminating in the plague of 1899. It is also possible that there may have been large-scale immigration of larvae from the west coast of France, in the years immediately prior to 1899. The crab and shell-fisheries were ruined by the hordes of hungry *Octopus* and fishermen were forced to seek alternative employment. On the English side there was no indication of a building up of the population before 1899, but from January of that year the species became increasingly plentiful, reaching its greatest abundance in 1900, causing widespread damage to the shell-fisheries by the end of the year. Garstang thought that the plague on the English coast was caused by dearth of food on the French side, resulting in 'migrations outwards from the overcrowded centres of multiplication'. This view is probably correct because a great many of the *Octopus* were large, reaching a span of 7 ft. from tip to tip of outstretched arms. These could not be less than 3 or 4 years old, and before 1899 there was no indication of an increase in the *Octopus* population.

The abundance of *Octopus* at Brighton in 1913 appears to be the outcome of favourable hydrographic conditions concentrating numerous larvae in the area in an earlier year. This was likely to be the year 1911 when a warm fine summer was experienced. I have no information on the prevalence of the species in Brittany and the Channel Islands for these years.

The second minor plague at Brighton, late in 1922, was obviously similar and probably linked with the more serious plague on the coast of Finistère in 1922.

In May 1948 a plague of young *Octopus* was reported at Brighton by the Press. These appear to have been mostly small specimens and may reasonably be regarded as brood of 1947, another favourable year for breeding.

Quite recently, January 1950, an increase of *Octopus* was reported from the Channel Islands, with the usual complaint from fishermen that they were

devouring the shellfish.[1] The exceptionally warm summers we have experienced in recent years have undoubtedly favoured the increase of *Octopus*.

The finding of a young *Octopus* on the beach at Montrose in Scotland can probably be attributed to the exceptional hydrographic conditions in the year 1893. In order to reach this point, the larva must have had an extended planktonic life in the North Sea. This raises the question whether benthic cephalopods with planktonic larvae are able to prolong their life in the plankton, in the same way as annelids, when the factors which induce 'settlement' are absent. It is possible that the Dublin Bay specimens were also carried beyond their normal range because of some unusual hydrographic conditions.

Summary

In Britain *Octopus vulgaris* occurs on the Channel coast and only very rarely on other coasts. In Brittany and the Channel Islands it frequently makes its lair at low water, but on the English side of the Channel it does not come so close inshore except in abnormal years of high sea temperatures.

The discovery of *Octopus* larvae of various sizes, from newly hatched to 6·0 mm. (mantle length), in plankton hauls taken to the north of the Channel Islands, proves that the species has a much longer planktonic life than hitherto supposed.

The water circulation in the English Channel, as indicated by drift bottles, is admirably suited to the dispersal of larvae to our shores from breeding centres on the coasts of Brittany and the Channel Islands.

Thus our *Octopus* population is believed to be an immigrant one maintained each year by an influx of larvae, and the vagaries of the water movements each year would account for the fluctuations in the abundance of the species.

Periodic plagues of *Octopus* appear to be due to good weather conditions over a succession of years causing a higher sea temperature, ensuring better breeding conditions for a warm water animal at the northern limit of its breeding range.

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EXPLANATION OF PLATES

PLATE I

Eggs of the Common Octopus (*Octopus vulgaris* Lamarck) spawned in an aquarium tank at Plymouth, March 1947. The strings of eggs hang from the roof of a small cave just large enough to contain the octopus. They were found and photographed when the tank was drained for cleaning.

PLATE II

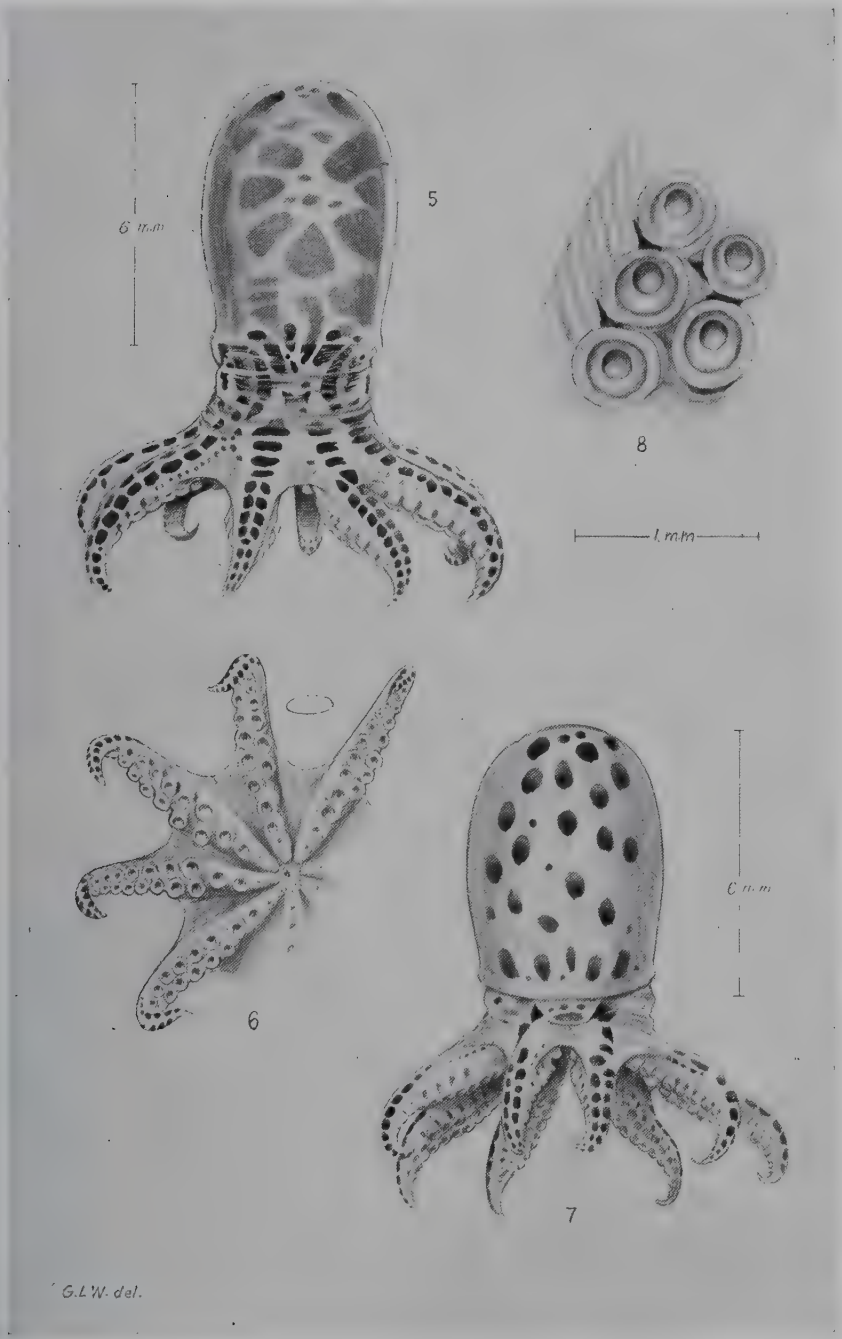
Figs. 1–4. *O. vulgaris* Lamarck; larvae from the English Channel; del G.L.W. Fig. 1. Dorsal view of larva of 2·4 mm. in ventral mantle length. Fig. 2. Ventral view of same specimen. Fig. 3. Dorsal view of larva of 3·15 mm. in ventral mantle length. Fig. 4. Lateral view of larva of 3·75 mm. in ventral mantle length.

PLATE III

Figs. 5–8. *O. vulgaris* Lamarck; the largest larva, [St. 72, 30. viii. 49; del G.L.W. Fig. 5. Dorsal view. Fig. 6. Oral face of web and tentacles. Fig. 7. Ventral view. Fig. 8. Enlarged view of arm suckers.

Photo by D. P. Wilson

Figs. 1–4.



Figs. 5–8.

THE SEASONAL VARIATION IN THE CELLULOSE CONTENT OF THE COMMON SCOTTISH LAMINARIACEAE AND FUCACEAE

By W. A. P. Black, B.Sc., Ph.D., F.R.I.C.

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(Text-figs. 1–6)

Introduction

Algal cellulose appears to have been relatively little studied and there is no information as to its seasonal variation in the brown marine algae. A study of the literature reveals numerous contradictions. In 1884, Stanford indicated in a report on alginic acid that he had obtained pure cellulose representing 10–15% of the air-dried plant.

Kylin (1915) showed that algal cellulose gave the characteristic colour reaction with iodine and sulphuric acid. He boiled the material in turn with 1·25% sulphuric acid and 1·25% sodium hydroxide and called the insoluble residue cellulose.

In 1926, Atsuki & Tomodo obtained a crude fibre figure of 6% for *Laminaria saccharina*, but stated that the greater part of the crude fibre of the laminarias consisted of the hemicelluloses and that there was so far no evidence of the normal cellulose.

Ricard (1931) removed the alginic acid with sodium carbonate, then treated the residue with dilute boiling solutions of sulphuric acid and potassium hydroxide. The hydrolysis of the residual material with sulphuric acid gave only traces of reducing sugars, and the author did not regard it as cellulose but called it algulose. *L. flexicaulis* contained 4·3–7·6% of this material and *L. saccharina* 2·8–10·9%.

Dillon & O'Tuama (1935), however, isolated cellulose from the brown algae. The residue after the removal of alginic acid with dilute ammonia was treated with dilute hydrochloric acid and then several times with boiling 5% sodium hydroxide. It was finally washed with alcohol and ether, and was shown to have the properties of cellulose. On hydrolysis with hydrochloric acid it gave glucose characterized by the isolation of the glucosazone, and with carbon disulphide it formed a viscose resembling the viscose from ordinary cellulose. They also prepared acetylated and methylated compounds with properties similar to those of the corresponding derivatives of ordinary cellulose.

Russel-Wells (1934) determined the crude fibre content of various algae and showed by its solubility in cuprammonium hydroxide and by its acetate that this fibre was cellulose.

Viel (1939) carried out a systematic study of the celluloses from *Fucus vesiculosus* (2·10%), *F. serratus* (2·81%), *Laminaria saccharina* (6·9%) and *L. cloustoni* (5·04%). Analysis showed the carbon-hydrogen percentages to be remarkably similar and in agreement with $(C_6H_{10}O_5)_n$. Hydrolysis gave 90% glucose, while thermal fractionation of the products of pyrogenation gave graphs comparable with those of previously studied vegetable celluloses.

Recent work by Percival & Ross (1949) has shown conclusively that algal cellulose is essentially the same as cotton cellulose. Hydrolysis with 72% sulphuric acid gave only D-glucose. Cellobiose octa-acetate was prepared by acetolysis indicating the presence of 1:4-β-linkages. Determinations by periodate oxidations indicated a chain length of 160 units, but the original cellulose was no doubt degraded during isolation. Finally, X-ray diagrams of algal cellulose showed the characteristic pattern of normal cellulose.

Experimental

The samples analysed were those taken in 1946 and previously reported by the writer (1948*a*,*b*, 1949). The cellulose was estimated as follows.

Ground seaweed (2 g.) was boiled under reflux with sulphuric acid (200 ml., 1·25%) for 30 min., filtered by suction through a 1 × 2 Gallenkamp sintered glass crucible, washed free from acid with water, and the residue boiled with sodium hydroxide (200 ml., 1·25%). After boiling in this way for 30 min., the solution was filtered through the 1 × 2 crucible and washed with water. The residue was removed from the crucible and kept overnight in chlorine water (100 ml. saturated), filtered on a weighed hardened paper, washed free from chlorine and washed on the filter with hot sodium hydroxide solution (50 ml. N/10). The residue was washed with water until free from alkali and finally with alcohol and ether, and then dried at 50° for 10 min. to give a white product which was weighed.

When applied to *Fucus* spp. the residue after treatment with boiling sodium hydroxide and chlorine water was often slimy and difficult to filter, and separation by centrifuging was necessary.

The results are given in Figs. 1–6.

Discussion of Results

General

Very little is known regarding the structure of the cell wall of the Phaeophyceae. Fritsch (1945) concludes that it consists of pectic substances with a layer giving the reactions of cellulose adjacent to the protoplast. In the brown algae the pectic substance is no doubt alginic acid which, with its long

chain structure, will give flexibility to the plant. To withstand wave-action such a structure is probably reinforced with cellulose, and the results of this investigation show that the cellulose content increases with the depth of immersion, when additional strength is required by the plant.

Very little is known, also, regarding the metabolism of the brown algae, but in the absence of any reducing sugars, it would appear that mannitol is probably the primary product of photosynthesis. In 1933, Khouvine showed that cellulose could be synthesized from mannitol by *Acetobacter xylinum*, and quite independently Barsha & Hibbert (1934) obtained the same results and showed that the cellulose membranes were chemically identical with cotton cellulose. In the brown algae, therefore, mannitol is probably the precursor of the cellulose.

The Laminariaceae

Laminaria cloustoni

In Fig. 1 the graphs for the stipe, the frond and the whole plant show that the cellulose content on the anhydrous basis exhibits two maxima and two minima in the year. Similar graphs have been obtained for several of the other constituents (Black, 1948*a*,*b*, 1949) and for the diatom periodicity, and sometimes there is a correlation with the nutrient content of the water and the periods of rapid and slow growth (Black & Dewar, 1949).

In March, when the new frond is forming, the cellulose is at a maximum of 5·76% in the frond and 10·27% in the stipe. From March to June/July a period of rapid growth occurs with an increase in the mannitol content while the cellulose content decreases. This may be due to the accumulation of mannitol in the whole plant or to elongation during rapid growth. From June to August/September during the period of slow growth, when the nutrients are absent from the sea water, the cellulose content increases again, while at the same time laminarin is also increasing (Black, 1948*a*). In September, when the nutrients are again regenerated in the sea water, there is probably a second period of growth and a decrease in the cellulose content occurs. It would appear, therefore, that when the results are expressed on the anhydrous basis a correlation exists between the cellulose content and the periods of rapid and slow growth. When the results, however, are calculated on the wet basis (Fig. 2) two maxima are again recorded, one in February/March and the other from September to November. On the dry basis the cellulose content begins to fall in April and continues to fall until June; on the wet basis it is constant and at a minimum from April to June, due to the dry weight increasing with a rapid increase in mannitol. From June to November the cellulose on the wet basis increases while on the dry basis it begins to decrease in September, the increase in dry-weight content now being due to an increase in laminarin. A rapid decrease then occurs in December, the period of sporogenesis of this species, and this is probably accompanied by an increase in the uptake of water, as there is a considerable decrease in the dry-matter content both in

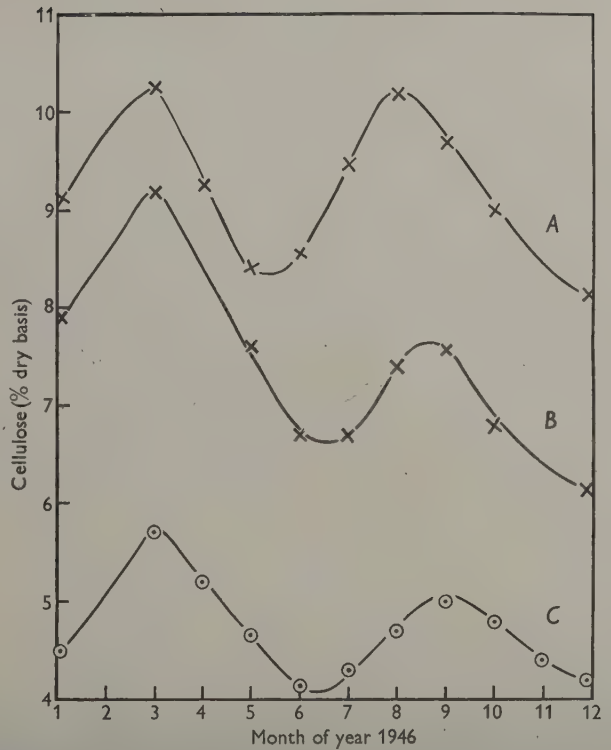

Fig. 1. Seasonal variation in the cellulose content of *Laminaria cloustoni* (dry basis): (*A*) in the stipes; (*B*) in the whole plant; (*C*) in the fronds.

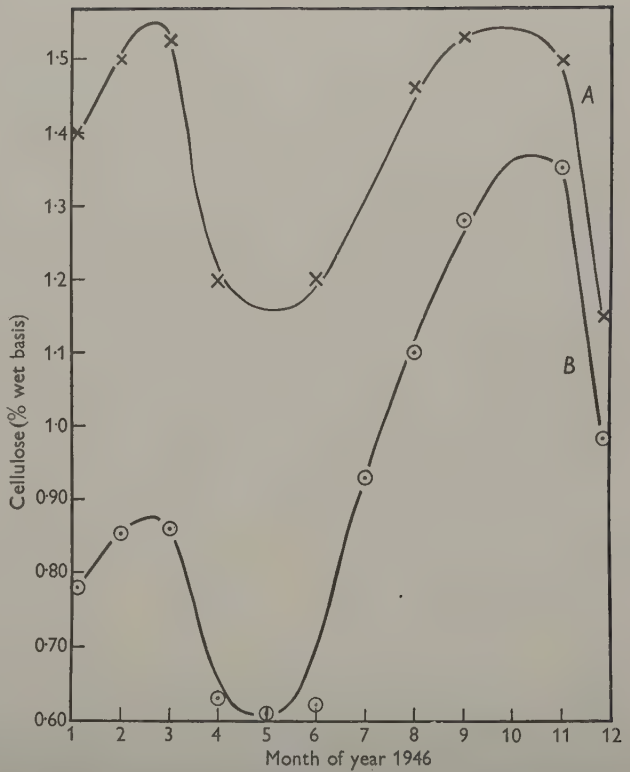

Fig. 2. Seasonal variation in the cellulose content of *Laminaria cloustoni* (wet basis): (*A*) in the stipes; (*B*) in the fronds.

stipe and frond, which explains the rapid decrease on the wet basis while there is little change on the dry basis. On the wet basis, therefore, there would appear to be a correlation between the cellulose content and the reproductive cycle of the plant.

Laminaria saccharina

In this species the cellulose content (dry basis) of the frond (4–5%, Fig. 3) is of the same order of magnitude as that of *L. cloustoni* frond (Fig. 1), but the stipes contain less cellulose (7–8%) than those of *L. cloustoni* (8·5–10%). Considerably less seasonal variation occurs in this species, but despite this the two maxima are apparent in the year and occur at approximately the same time as those of *L. cloustoni.*

Laminaria digitata.

The cellulose content of this species (Fig. 4) undergoes a similar seasonal variation to that of *L. saccharina*, with the exception of the loch frond samples in which the variation is between 3 and 5%. In general, however, the graphs are very similar and exhibit two maxima in the year and a distinct minimum in July.

The cellulose graphs on a wet basis for *L. saccharina* and *L. digitata* have been omitted. The only outstanding feature in both species is that the graphs for the open-sea samples show less seasonal variation (0·5–0·7%) than those for the loch samples (0·5–1·0%). This is due to the marked seasonal variation in dry matter which occurs in the loch samples as the result of the accumulation of laminarin. This is in agreement, to a certain extent, with the theory that the cellulose content can be correlated with the periods of growth. At Atlantic Bridge the *L. digitata* frond grows to a length of 7–8 ft. (213–244 cm.), growth appears to continue throughout the summer and there is very little laminarin formed. The dry weight shows little change and there is no marked variation in the cellulose content. On the other hand, in Loch Melfort, the *L. digitata* frond only grows to a length of about 2–3 ft. (61–91 cm.), laminarin accumulates and there is a marked increase in the dry-matter content. It appears, therefore, that laminarin is formed when photosynthesis can proceed, but some other factor is limiting growth.

The Fucaceae

With the exception of *Fucus spiralis*, which contains approximately 4·5% of cellulose (dry basis) throughout the year, there appears to be a correlation between the cellulose content of the Fucaceae and the depth of immersion of the species, the cellulose increasing from about 1% in *Pelvetia canaliculata* to 2–2·5% in *Fucus serratus* and *F. vesiculosus*. On the anhydrous basis the cellulose content of *Pelvetia canaliculata*, *Ascophyllum nodosum* and *Fucus spiralis* remains relatively constant throughout the year (Fig. 5). But when the results

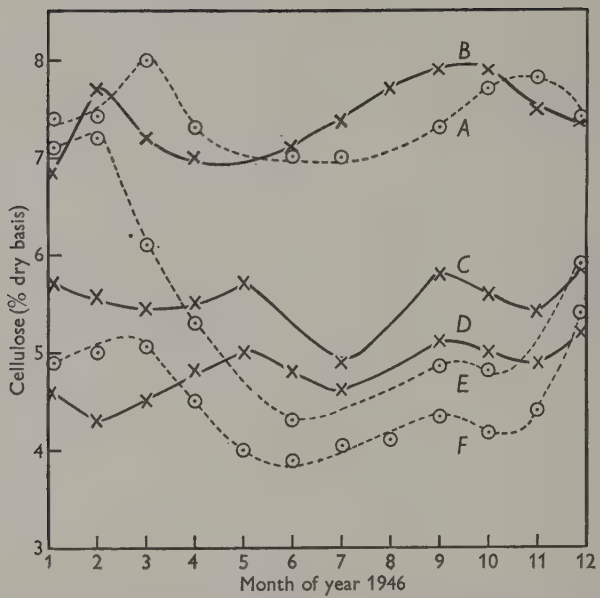

Fig. 3. Seasonal variation in the cellulose content of *Laminaria saccharina* (dry basis): (*A*) in the open-sea stipes; (*B*) in the loch stipes; (*C*) in the loch whole plants; (*D*) in the loch fronds; (*E*) in the open-sea whole plants; (*F*) in the open-sea fronds.

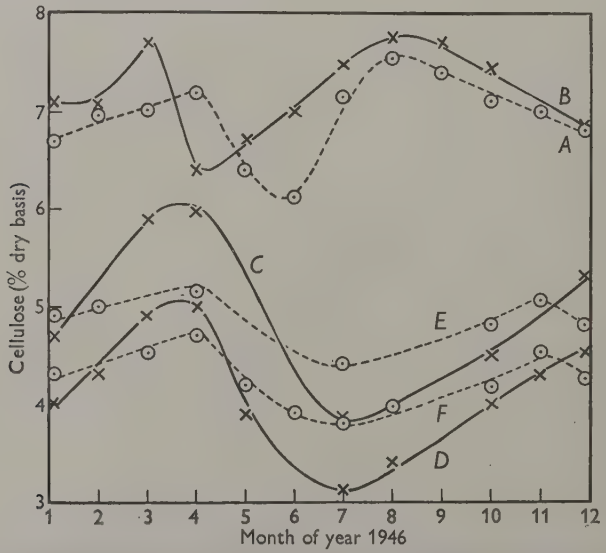

Fig. 4. Seasonal variation in the cellulose content of *Laminaria digitata* (dry basis): (*A*) in the open-sea stipes; (*B*) in the loch stipes; (*C*) in the loch whole plants; (*D*) in the loch fronds; (*E*) in the open-sea whole plants; (*F*) in the open-sea fronds.

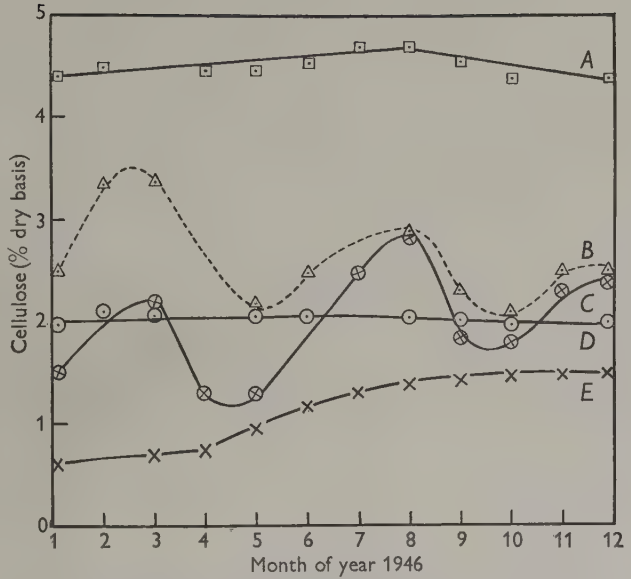

Fig. 5. Seasonal variation in the cellulose content of the Fucaceae (dry basis): (*A*) *Fucus spiralis*; (*B*) *F. serratus*; (*C*) *F. vesiculosus*; (*D*) *Ascophyllum nodosum*; (*E*) *Pelvetia canaliculata*.

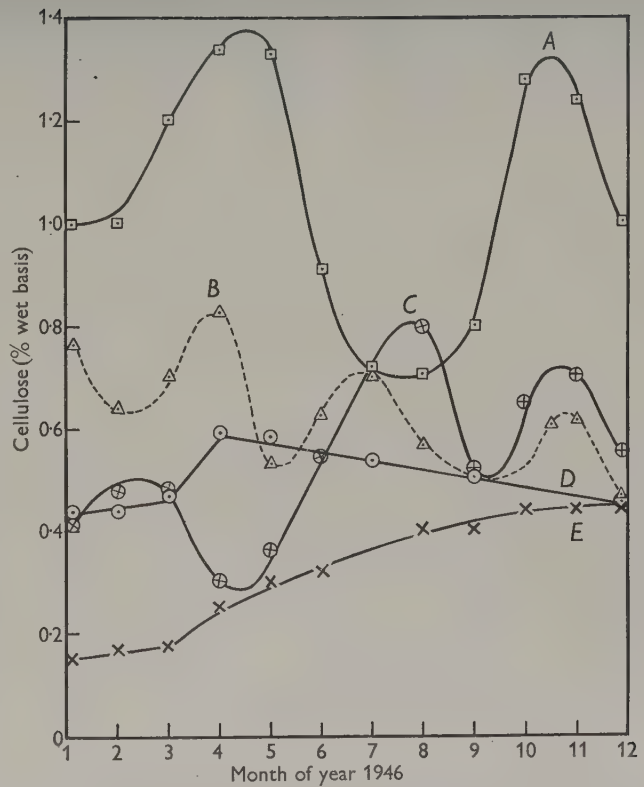

Fig. 6. Seasonal variation in the cellulose content of the Fucaceae (wet basis): (*A*) *Fucus spiralis*; (*B*) *F. serratus*; (*C*) *F. vesiculosus*; (*D*) *Ascophyllum nodosum*; (*E*) *Pelvetia canaliculata*.

are expressed on the wet basis the graphs for *Pelvetia canaliculata* and *Ascophyllum nodosum* (Fig. 6) show no change of form, an increase in cellulose in the dry matter accompanying an increase in the dry weight. This is not true, however, in *Fucus spiralis*, for although the proportion of cellulose in the dry matter remains constant the dry-matter content undergoes considerable seasonal variation. The graph for *F. spiralis* (wet basis), therefore, shows marked seasonal fluctuations (Fig. 6). This species takes in a quantity of water during June/July to assist in liberating its gametes, and at this time of the year the fertile tips are considerably swollen and full of mucilage and the dry-weight content of the whole plant is considerably reduced.

With *F. serratus* and *F. vesiculosus* the graphs on the wet basis are approximately parallel to those for the dry basis indicating that the cellulose contributes to the increase in dry matter of the plant. The minima obtained in May/June and October/November may be due to rapid growth at that time and/or an increased uptake of water by the plant preparatory to sporing.

The writer wishes to thank Miss B. Graham and Mr W. Cornhill for assistance with the analytical work, and Dr E. G. V. Percival and Dr A. G. Ross of Edinburgh University for the details of the method.

Summary

Monthly samples of the common British Laminariaceae and Fucaceae taken during 1946 have been analysed for cellulose.

The cellulose content has been found to increase with the depth of immersion of the weed.

In the Laminariaceae, both in the stipe and frond it undergoes marked seasonal variation, exhibiting two maxima, March/April and September/October with a distinct minimum in June/July.

In *Laminaria cloustoni*, in March, maxima of 5·7 (dry basis) occur in the fronds and 10·3% in the stipes with minima, in June, of 4·1 and 8·4% respectively. In *Laminaria saccharina* the cellulose content (dry basis) varies between 4–5% in the frond and 7–8% in the stipe and in *Laminaria digitata* between 3–5% in the frond and 6–8% in the stipe.

In the Fucaceae, on the dry basis, a similar seasonal variation occurs in *Fucus vesiculosus* (1·2–2·8%) and *F. serratus* (2·1–3·5%), but in *Ascophyllum nodosum* (2·0%), *Fucus spiralis* (4·4–4·7%) and *Pelvetia canaliculata* (0·6–1·5%) the cellulose content remains relatively constant throughout the year. When the results are calculated on the wet basis, graphs parallel to those for the dry basis are obtained, except in *Fucus spiralis*, in which the cellulose content undergoes marked seasonal variation in June/July, since this species takes in appreciable water preparatory to shedding its gametes.

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LISSOCLINUM ARGYLLENSE N.SP., A NEW ASCIDIAN FROM SCOTLAND

By R. H. Millar

The Marine Station, Millport

(Text-fig. 1)

In the summer of 1949 a compound ascidian was collected from the shore of Seil Island, Argyll. This proved to be a new species of the family Didemnidae. It is proposed to name it *Lissoclinum argyllense*, the specific name indicating the area in which it was first found. No species of *Lissoclinum* has hitherto been included in the British fauna.

Occurrence. Colonies have been found round the shores of Seil Island, Argyll, and on the shore at Salen in the Isle of Mull, Argyll. All colonies were on the under sides of stones in the intertidal zone. They were not common, except locally, where several colonies sometimes occurred within a few yards of each other.

The colony (Fig. 1A) is usually pure white but is sometimes tinged with pink or buff. It forms encrusting sheets up to 50 mm. in diameter and about 2 mm. thick. The colony is rather flaccid and the upper layer of the test can be easily torn away from the lower layer. The oral openings (Fig. 1A, *Or.op.*), which are scattered evenly over the surface, are round and more conspicuous than those on the colony of *Didemnum maculosum* (Edwards), with which the present species might be confused. Cloacal openings (Fig. 1A, *Cl.op.*) are also conspicuous and are round or elliptical. The cloacal cavities are very greatly developed within the colony and leave little more than a thin upper and lower layer of test between which the zooids are stretched. In these upper and lower layers spicules are densely packed, giving the colony its white appearance. The zooids are arranged in the colony in irregular rows.

The spicules (Fig. 1B) are of a very characteristic shape, which at once distinguishes them from those of *Didemnum*. In optical section they show four to six rays, which are not conical and pointed as in *D. maculosum*, but have instead a broad end with two or three rounded prominences. The spicules are 0·03–0·05 mm. in diameter. They somewhat resemble the spicules of *D. perforatum* (Giard).

The zooid (Fig. 1C) is about 1·8 mm. long. The oral siphon has six short pointed equal lobes. There is no atrial siphon. The atrial opening, which is without a languet, is very large and extends round the thorax to near the endostyle, so exposing nearly the whole branchial sac. The tentacles number

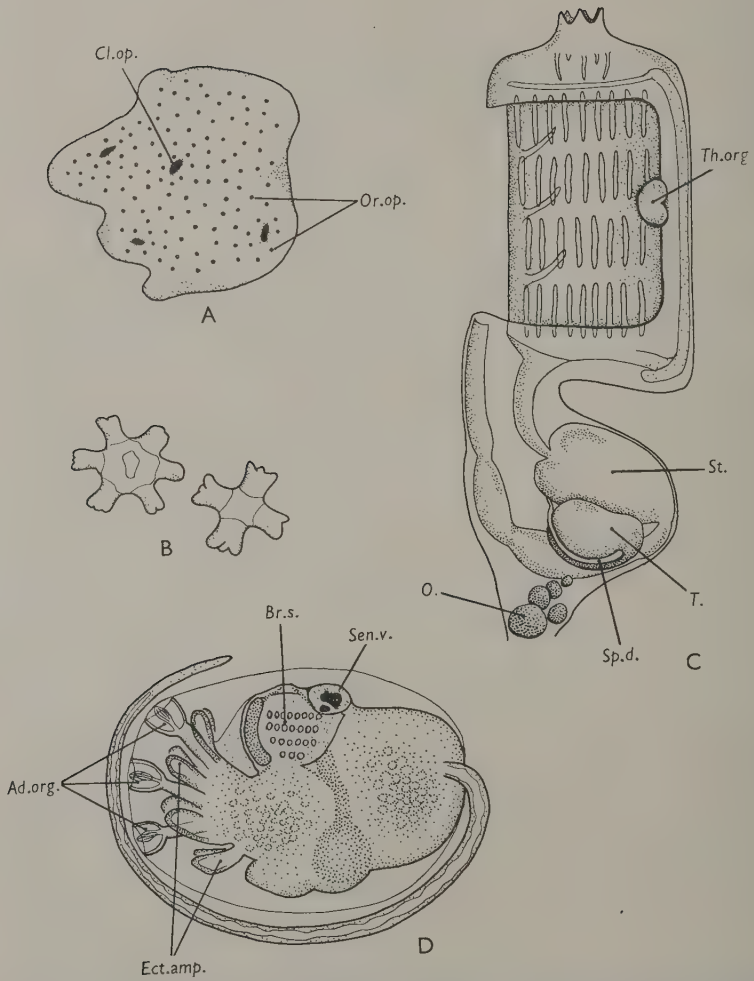

Fig. 1. *Lissoclinum argyllense* n.sp. A, colony; B, spicules; C, zooid, seen from the right; D, larva, seen from the left. *Ad.org.*, anterior adhesive organs; *Br.s.*, rudiment of the branchial sac; *Cl.op.*, cloacal opening; *Ect.amp.*, ectodermal ampullae; *O.*, ovary; *Or.op.*, oral openings; *Sen.v.*, sensory vesicle; *Sp.d.*, sperm duct; *St.*, stomach; *T.*, testis; *Th.org.*, lateral thoracic organ.

up to 24 and alternate in size. There are four rows of stigmata in the branchial sac, each row having eight or nine stigmata. The three dorsal languets of the pharynx are quite large. A lateral thoracic organ (Fig. 1 C, *Th.org.*) is present on each side of the body, on the ventral margin of the atrial opening, between the second and third rows of stigmata. Beside each thoracic organ is a large mass of spicules. The abdomen is shorter than the thorax and contains the slightly curved oesophagus, the ovoid smooth-walled stomach (Fig. 1 C, *St.*), the intestine divided into three long chambers, and the rectum extending to the level of the fourth row of stigmata. In the intestinal loop is a single large round testis (Fig. 1 C, *T.*). The sperm duct (Fig. 1 C, *Sp.d.*) is not spirally coiled but passes round in a half circle to the lower side of the testis, where its origin is marked by a slight thickening. The ovary (Fig. 1 C, *O.*) has a string of ova extending from the lower part of the intestinal loop down into the common test below the abdomen. Apparently the ova in development pass down into the lower layer of common test, where the larvae are found. Asexual reproduction is by pyloric budding as in other didemnids.

Larvae (Fig. 1 D) were found in colonies collected in August and November, but may have been present in other months when no colonies were examined. The larvae were embedded in the lower layer of the common test. In general organization the larva of *Lissoclinum argyllense* resembles the larva of other didemnids. It measures 0·6 mm. from the end of the adhesive organs to the base of the tail. The sensory vesicle (Fig. 1 D, *Sen.v.*) has a small ovoid static organ on the floor and a larger ocellus on the posterodorsal wall. The rudiment of the branchial sac (Fig. 1 D, *Br.s.*) has four horizontal rows of stigmata and a vertical endostyle. At the anterior end of the larva there are eight ectodermal ampullae (Fig. 1 D, *Ect.amp.*) and a vertical row of three adhesive organs (Fig. 1 D, *Ad.org.*).

Systematic position. This new species shows the common characteristics of the family Didemnidae, into which it falls naturally. The genera of this family are divisible into two groups identified thus:

(*a*) The proximal part of the sperm duct always spirally coiled; the common cloacal cavities generally not greatly developed.

(*b*) The proximal part of the sperm duct never spirally coiled; the common cloacal cavities often greatly developed.

The second group contains *Diplosoma* (Macdonald), *Lissoclinum* (Verrill), and *Echinoclinum* (Van Name), and to it the new species belongs. It is excluded from *Diplosoma* by the possession of spicules, and from *Echinoclinum* by the shape of the spicules. It agrees closely with *Lissoclinum* in all features examined except in its undivided testis. All species of *Lissoclinum* hitherto described have two or more testis follicles. Thus *L. aureum* Verrill has five to ten follicles, most species have two follicles, and *Echinoclinum*, which Van Name (1945) is inclined to regard as a subgenus of *Lissoclinum*, has the testis only partially divided into two by a deep groove. *L. argyllense*, with its undivided

testis, appears to stand at one end of this series. By including the new species in *Lissoclinum* we expand the definition of that genus to include forms with an undivided testis.

REFERENCE

VAN NAME, W. G., 1945. The North and South American ascidians. *Bull. Amer. Mus. Nat. Hist.*, Vol. 84, 476 pp.

THE BIOLOGY OF THE SMALL PLANKTONIC COPEPODS OF PLYMOUTH

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From the Marine Laboratory, Plymouth

(Text-figs. 1–13)

CONTENTS

	PAGE
Introduction	393
Material and methods	394
Presentation of data	395
Hydrography and phytoplankton	396
Abundance and reproduction near Plymouth	397
Pseudocalanus elongatus	397
Paracalanus parvus	399
Centropages typicus	401
Temora longicornis	402
Acartia clausi	402
Oithona similis	405
Oithona nana	405
Oncaea venusta	405
Corycaeus anglicus	405
Other species	405
Size near Plymouth	409
Distribution and size in adjacent waters	410
Discussion	411
Summary	415
References	416
Appendix (Tables I–XX)	417

Introduction

The following paper describes investigations carried out on the life histories of the smaller plankton copepods in the Plymouth area during 1947. A large number of investigations have been carried out on the life history of *Calanus*, but our knowledge of the other species is meagre. What knowledge exists is mainly due to the work of Fish (1936*a–c*) in the Gulf of Maine, Wiborg (1940, 1944) in Oslo Fjord and the Nordåsvatn, a partly enclosed body of water near Bergen, and Marshall (1949) in Loch Striven. The differences in hydrography and other conditions made it desirable that a similar study should be carried out at Plymouth.

The species considered are: *Paracalanus parvus* (Claus), *Pseudocalanus elongatus* Boeck, *Centropages typicus* Krøyer, *Temora longicornis* (O. F. Müller), *Oithona similis* Claus, *O. nana* Giesbrecht, *Oncaea venusta* Philippi, and *Corycaeus anglicus* Lubbock.

All but the last three (*Oithona nana*, *Oncaea* and *Corycaeus*) were most abundant in the spring and summer; the last three were abundant at the end of

the year, accompanied by the harpacticid *Euterpina acutifrons* (Dana). Only very small numbers of species other than the above were taken.

This work was carried out at the Marine Laboratory, Plymouth, during the tenure of a grant from the Development Commission. I wish to record my thanks to Mr F. S. Russell, F.R.S., for his inspiration and encouragement in this work, and for making freely available all the facilities of the laboratory, to Dr H. W. Harvey, F.R.S., for loan of measuring nets, and to Capt. W. H. Creese and the crew of the '*Sabella*' for their care in taking my samples in all weathers.

Material and Methods

Area. The bulk of the samples were taken at the Station L 4, 5 miles from Plymouth breakwater, where there is an average depth of a little over 50 m. A few samples were taken a mile or two outside the breakwater (Table I), and in addition three short cruises were undertaken to investigate the state of the copepod population in the surrounding waters.

Nets used. Most of the samples were taken with Harvey measuring nets fitted with a silk net of 200 meshes to the inch (Harvey, 1934, 1935). Additional hauls were made with various tow nets and with a Clarke-Bumpus plankton sampler (Clarke & Bumpus, 1940). All hauls at L 4 (except those with the plankton sampler) were made vertically, fishing through all but the lower 1 or 2 m. of the water column. Normally between 1 and 3 $m.^3$ of water were passed through the net. In the cruises, the hauls were made vertically from 50 m. to the surface. The quantitative results are based on samples taken with the later model of the Harvey net (Harvey, 1935) until 6 August, when the instrument was unfortunately lost. After that date the earlier net (Harvey, 1934) was used, and later the calibration was checked and found identical to the original calibration made by Harvey (1934). The calibration of the net used first was never checked, but as the meter was in good order it is probable that it had not altered more than a small amount. Two quantitative samples are utilized that were taken with the Clarke-Bumpus sampler. For these, the published calibration was used. Thus all counts for quantitative purposes were based on known volumes of filtered water.

Subsampling. Samples were subsampled by an adaptation of the method described by Russell (1931). During the spring and summer months when the small stages were very numerous it was necessary to divide the samples into coarse and fine fractions by passing through sieves, subsampling to deal with a small amount of the fine fraction and a larger amount of the coarser fraction. The exact degree of subsampling for each catch and each species is given in Table I. The species and stages were counted and measured on a squared slide under a microscope fitted with a mechanical stage and micrometer eyepiece, of which one division represented $17{\cdot}7\,\mu$. Measurements are comparable with those of Marshall (1949), representing length of cephalothorax.

Identification of stages. Full use was made of the papers by Oberg (1906) and Kraefft (1910) for distinguishing the nauplii and copepodite stages respectively. *Microcalanus* was not present in any number at Plymouth, so the distinction between the nauplii of *Paracalanus* and *Pseudocalanus* was easy to make on size alone.

A certain number of *Centropages hamatus* occurred. No distinction was drawn between the nauplii of these two species, but in view of the numerical superiority of *typicus* all the *Centropages* nauplii are lumped as belonging to that species, whereas some were undoubtedly *hamatus* nauplii.

The nauplii of *Oithona similis* and *O. nana* were confused in the early part of the year, when few *nana* were present, but in the later part of the year the distinction became obvious and the nauplii were separated. The nauplii of *nana* were smaller and altogether more slender than those of *similis*.

There appears to be no account of the stages of *Oncaea* or *Corycaeus*, and here these two species are separated into males, females and juvenile individuals. They were accompanied by large numbers of nauplii which were counted *in toto*: they probably comprised nauplii of these two species together with possibly *Euterpina* and other harpacticids. *Metridia lucens* was encountered in a cruise to the west of Plymouth, although it was not met with at Plymouth. The stages were worked out, and found to agree with the usual pattern.

Presentation of Data

With most of the species under consideration, all stages from nauplii to adults were found throughout the year. Conclusions as to number of generations passed through therefore rest on the comparative abundance of the different stages, the percentage distribution of the stages, and the sizes of the adults. Each of these methods has its disadvantages, and it is necessary to draw conclusions from all three lines of evidence together.

Absolute numbers, presented as abundance graphs, suffer from the disadvantage that if the water is patchy, with rich and poor areas, an abundance of nauplii encountered during one week does not necessarily give rise to the expected abundance of adults a few weeks later. They have the advantage, however, of showing the stock as it actually occurs.

Percentages of stages reveal the state of affairs in patchy water to a much better degree than do abundance figures. However, if the nauplii vary in number from one sample to another over a wide range, the percentage figures of the adults bear little relation to their numbers, but reflect the changes in the numbers of nauplii. Thus a peak of nauplii will apparently be followed by an increase in adults, while in actual fact the numbers of adults may decline, to a lesser extent, with the numbers of nauplii.

Size-groups of adults possibly present the most reliable evidence of separate generations, where such differences in size exist. Size differences do not

always occur, however; in the later part of the year successive generations of adults would appear to have arisen, in some species, with little difference in size, generations being separable on other grounds.

Conclusions as to number of generations must therefore be drawn from all these sources. In the diagrams given, the percentage and size-group graphs are mounted beneath the abundance graphs, and the interpretation that appears most probable is placed below them all.

In the abundance graphs, the nauplii are illustrated in a scale which is one-tenth of that of the copepodites. In the percentage figures, the divisions are taken as: nauplii, copepodites I–III, IV–V, and VI. This is the grouping used by Fish (1936*a*, *b*, *c*) and is sufficient to show the main features.

The size-group graphs are reproduced in such a way that one individual measurement is reproduced as one unit on the figure, the numbers not being reduced to percentages. This has the advantage that use can be made of small numbers, such as occur, for instance, in *Temora* and *Acartia* in winter, which are concrete evidence but are not plentiful enough to make into percentage figures. The vertical scales are varied for convenience according to the species.

The method of suggested interpretation is adapted from Russell (1935). The different levels of the parts of the diagram representing adults of different size; the mid-line of a particular adult block is more or less the average size of the group concerned, and is a very rough replica of the adult figure of the abundance graph. The successive generations of nauplii in the interpretation are a rough replica of the naupliar peaks in the abundance graph.

Hydrography and Phytoplankton

The hydrographic conditions and phytoplankton of the area around L4 have been made the subject of many publications. For phytoplankton conditions, see Harvey, Cooper, Lebour & Russell (1935), and Mare (1940). No phytoplankton counts or pigment assessments have been made in connexion with this study. Temperatures were taken at 1 and 30 m. with an insulated water-bottle, supplemented on occasion by surface temperatures taken by bucket from further in-shore (Table I).

To compare the temperatures for 1947 (Fig. 1) with those in 1934, when the combined study was made on the various aspects of the phyto-zooplankton relationships (Harvey *et al.*, 1935) we may note the following differences. In 1947, the winter minimum temperatures at the beginning of the year were roughly 5·5° C., or two degrees lower; the summer maximum was roughly 16·5° at 30 m., or two and a half degrees higher. Stratification set in towards the end of March, about 2 weeks earlier than in 1934, but broke up at about the same time, at the end of September. In 1947, the temperature at 30 m. had not attained its full value until the end of August; after which a slow

decrease occurred until the end of October, when it became more rapid. In 1934, however, the highest values were reached a month earlier.

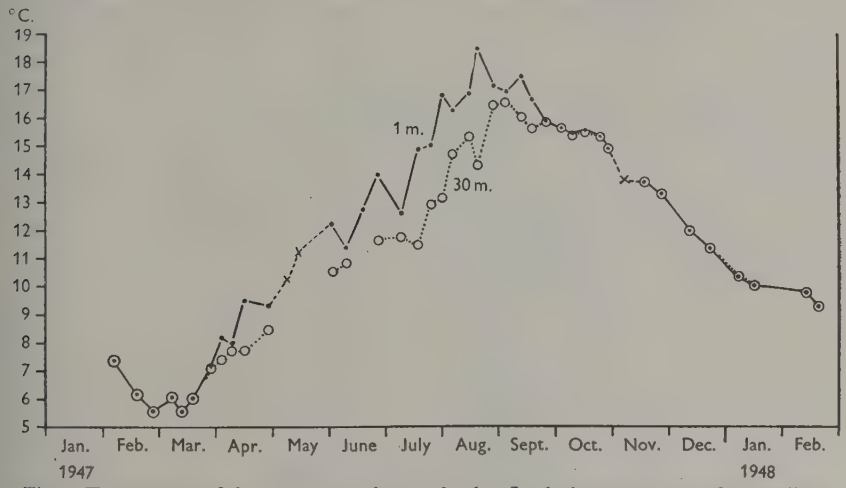

Fig. 1. Temperature of the water at 1 and 30 m. depth at L4 during 1947. ×, surface readings from closer in-shore

Abundance and Reproduction near Plymouth

Pseudocalanus elongatus (Fig. 2, Table II)

Abundant from March to October, greatest numbers from April to August.

The adult *Pseudocalanus* found early in the year (January and February) were of small size. Size-groups reveal that this population persisted until the end of March, when it died out. This population is here called the '0' generation. It was joined at the end of February by a population of adults of larger body size. This population received increments at progressively larger size, the early arrivals at the end of February being small and dying out in early April, the later members appearing in late March and early April and dying out by June. This '1' group appears to have been responsible for the large group of nauplii in May, which can be followed through the later developmental stages to adults in June. These adults were of a clearly different size, smaller than the adults '1' and are called adults '2'. The peaks in the abundance graph at mid-June and at the end of June were composed of individuals similar in size, and together they gave rise to the middle peak of abundance of nauplii at the end of June and beginning of July. It therefore seems most reasonable to consider this as one generation, although the abundance of late stages and percentages present a rather confused picture.

After this the generations became more merged, and large variations occurred in the total stock. It would appear from the percentage graph that

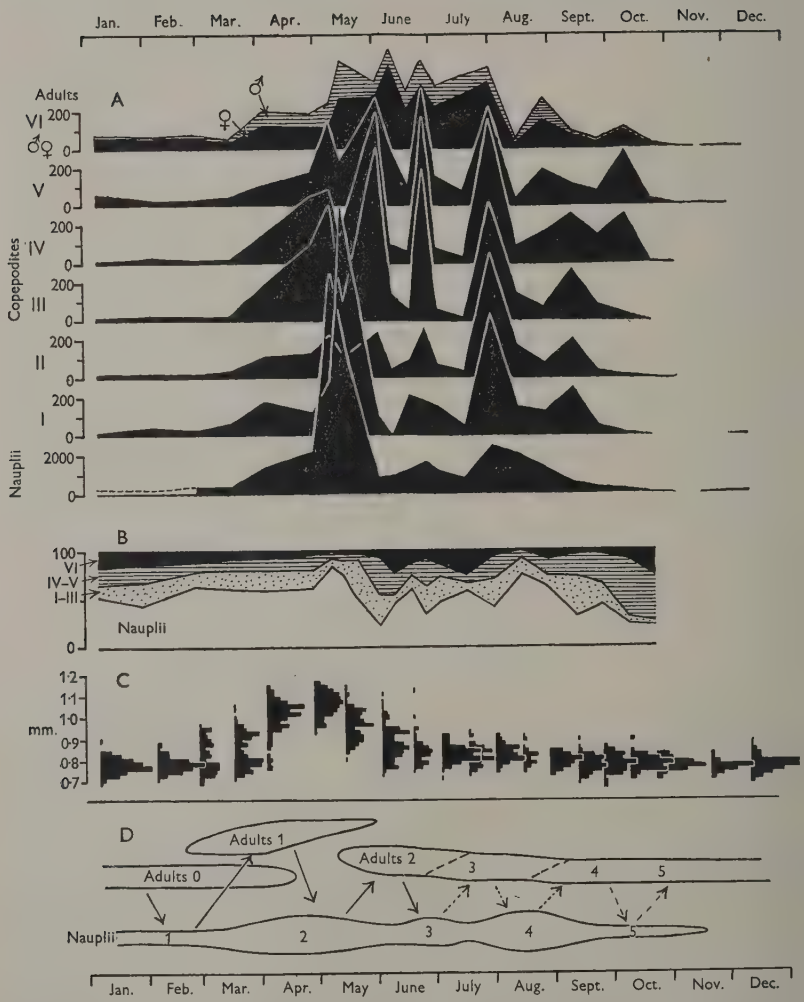

Fig. 2. *Pseudocalanus elongatus*. A, abundance of stages; B, percentage distribution of stages; C, size-groups of adult females; D, suggested interpretation.

these nauplii gave rise to adults '3' in July. These were not separable from the adults '2' on size. These adults were responsible for the third period of abundance of nauplii (nauplii '4' in the interpretation) during July and August, and these nauplii in turn gave rise to adults '4' in late August and September, of slightly smaller size than adults '3'.

Now the abundance figure for nauplii '4' here indicates only one extended period of abundance, but from consideration of the stages from copepodites 1 to adults, it is obvious that a further group developed from nauplii in early September to adults in October, and these nauplii appeared shortly after the development of adults of group '4'. This would appear therefore to make a fifth and last generation, apparent also from the percentage figure. The adults of this generation, however, are not obviously distinguishable from those of the previous generation by size.

In Loch Striven (Marshall, 1949) the course of generations was similar up to nauplii '2', when in the latter locality breeding became continuous to such an extent that individual generations could not be followed.

Paracalanus parvus (Fig. 3, Table III)

Abundant from end of April to December, greatest numbers from May to June and August to October.

Paracalanus showed a considerable degree of similarity to *Pseudocalanus*, the size-groups revealing populations of adults replacing each other in time with those of *Pseudocalanus*. It differed in that the size differences between adults of groups '2' and '3' were much more clearly marked, and the existence of a fifth group of adults is more certain. It would appear that an extra generation was passed through at the end of the year, when *Pseudocalanus* had ceased breeding. The march of the generations from the 'o' group adults as far as nauplii '3' was clear, but after this the broods were less well defined. In the abundance diagram, there is no clear transition from the nauplii '3' to adults of smaller size in August. It may be that the June nauplii did not survive, the eventual adult stock developing from the smaller numbers of nauplii present in July. It may be, on the other hand, that in June a different body of water moved over the station, water in which the development was at a slightly different stage. This delay in production of the next generation, whatever its cause, has been suggested in the interpretation by showing the adults '3' as not developing directly from nauplii '3'. The adults present during August, September and October were the adults '3' and '4', distinguishable in size groups. Adults '3' were smaller than those of generations '2' or '4'. Adults '3' and '4' gave rise to nauplii '4' and '5' in August and September. The nauplii present in November and December constitute yet another brood, the nauplii '6', which arose from an ill-defined group of adults '5'. This group was not distinguishable on size from adults '4', but its development can be traced through the copepodite stages on the abundance graph.

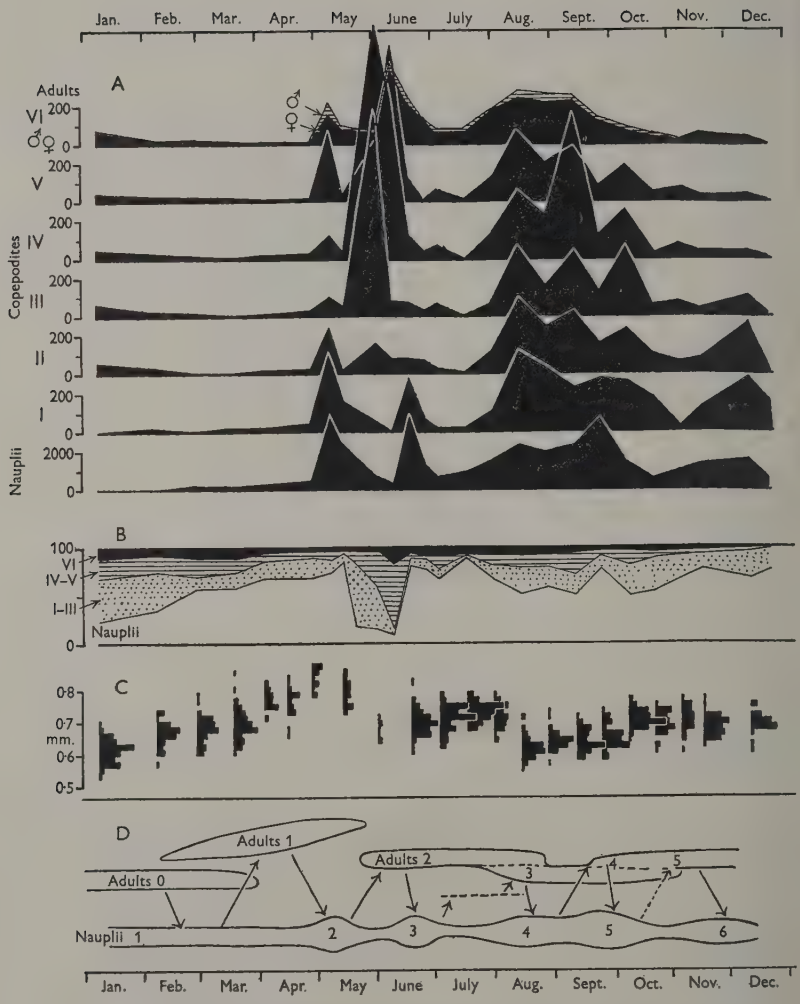

Fig. 3. *Paracalanus parvus*, A, abundance of stages; B, percentage distribution of stages; C, size-groups of adult females; D, suggested interpretation

Centropages typicus (Fig. 4, Table IV)

Few specimens of the genus *Centropages* were taken, most of them being *C. typicus*. Specific distinction between the nauplii of *typicus* and *hamatus* was not made, and because of its numerical superiority all the nauplii are included here as *typicus*. Although the numbers are small, the data are sufficient

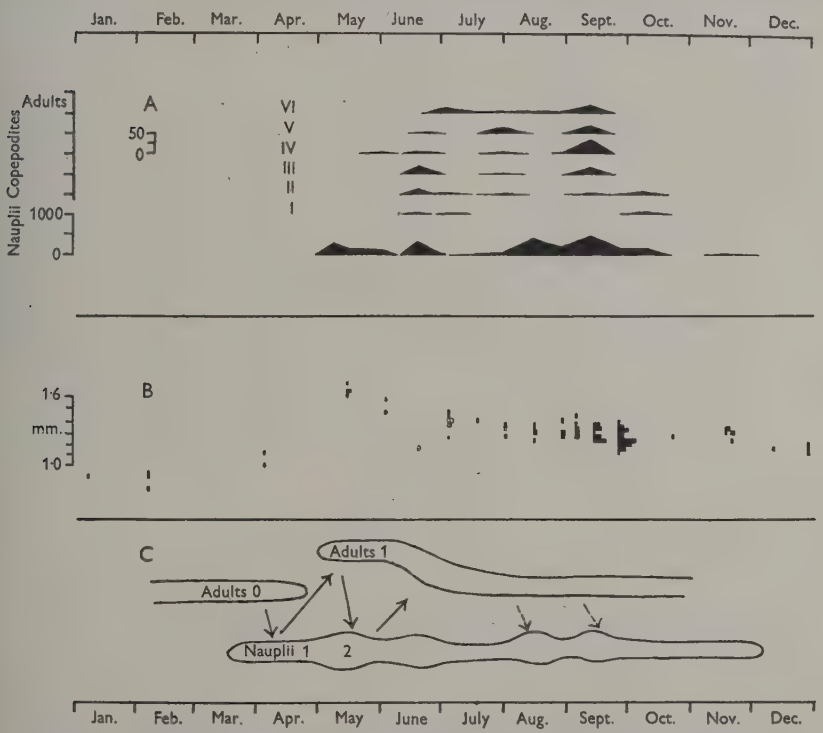

Fig. 4. *Centropages typicus*. A, abundance of stages; B, size-groups of adult females; C, suggested interpretation.

to show that *Centropages* nauplii were present from April to November, and the copepodite stages and adults were most abundant from June to September. The seasonal change in size was, so far as can be seen, similar to that in the other species, and groups of adults '0', '1' and '2' are suggested. The data are not sufficient to separate other generations, but the general similarity between the fragmentary picture obtained in this manner and the clearer pictures for *Temora* and *Acartia*, suggest the occurrence and course of generations to be somewhat similar.

Temora longicornis (Fig. 5, Table V)

Abundant from April until September, with a first maximum in May and June and a second in August and September.

The adult and copepodite stages of *Temora* were very scarce early in the year. Nauplii, however, were found in the plankton from February onwards. Because of the scarcity, the evidence as to size early in the year is scanty, but it is sufficient to show that, as in the other species, the size-groups change early in the year, indicating a new population of adults '1' appearing from February onwards.

This population was apparently responsible for the large peak of nauplii in May, the nauplii '2' which, in the abundance graph, can be seen developing to adults '2' in late May and June. Generations followed clearly, adults '3' appearing in July and adults '4' in late August. Nauplii and early copepodites were present in some numbers at the end of September and beginning of October, and these were probably the offspring of adults '4'. At this time of the year the development stages of *Temora* became swamped in numbers by other species, but specimens of adults measured in October, November and December indicated a population of adults of a slightly larger size than those of generation '4'; they were probably adults '5' which developed from nauplii in September and October. These were probably the overwintering adults.

Temora was thus very similar to *Pseudocalanus* and *Paracalanus* in the number of generations, but differed in being comparatively more scarce in the winter months. In addition, its generations were more clear-cut, breeding being less confused than in the other species.

Acartia clausi (Fig. 6, Table VI)

Abundant from April until October, with maximum numbers in May, June and July.

The course of generations of *Acartia* appears to have been very similar to those of *Temora*. Like *Temora*, it was scarce in the winter months. Specimens measured from January to March indicated a group of adults of small size, too sparse to be noticed in the abundance graph. These were joined in April by a larger group, the adults '1', and these latter were responsible for the large group of nauplii, the nauplii '2', at the end of April and beginning of May. These developed to adults '2' early in June. Generation '3' followed, with nauplii in June and adults in July and August. Generation '4', with nauplii in early August, developed to adults, distinguishable by size from those of '3', in late August and September. A further period of abundance of nauplii in September, the nauplii '5', cannot be seen to develop. All stages were present in small numbers in late November and December, and although there is no evidence for it here, it would appear possible, by comparison with *Temora*, that adults '5' arising from nauplii '5' might give rise to nauplii '6' in November.

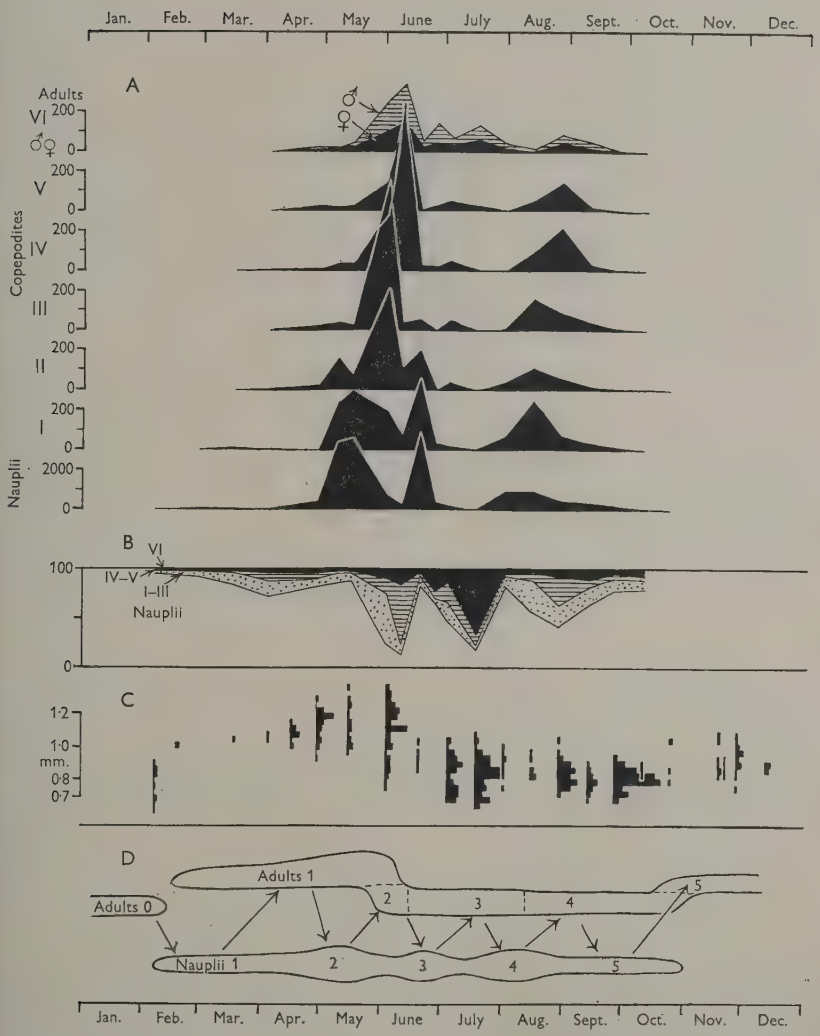

Fig. 5. *Temora longicornis*. A, abundance of stages; B, percentage distribution of stages; C, size-groups of adult females; D, interpretation.

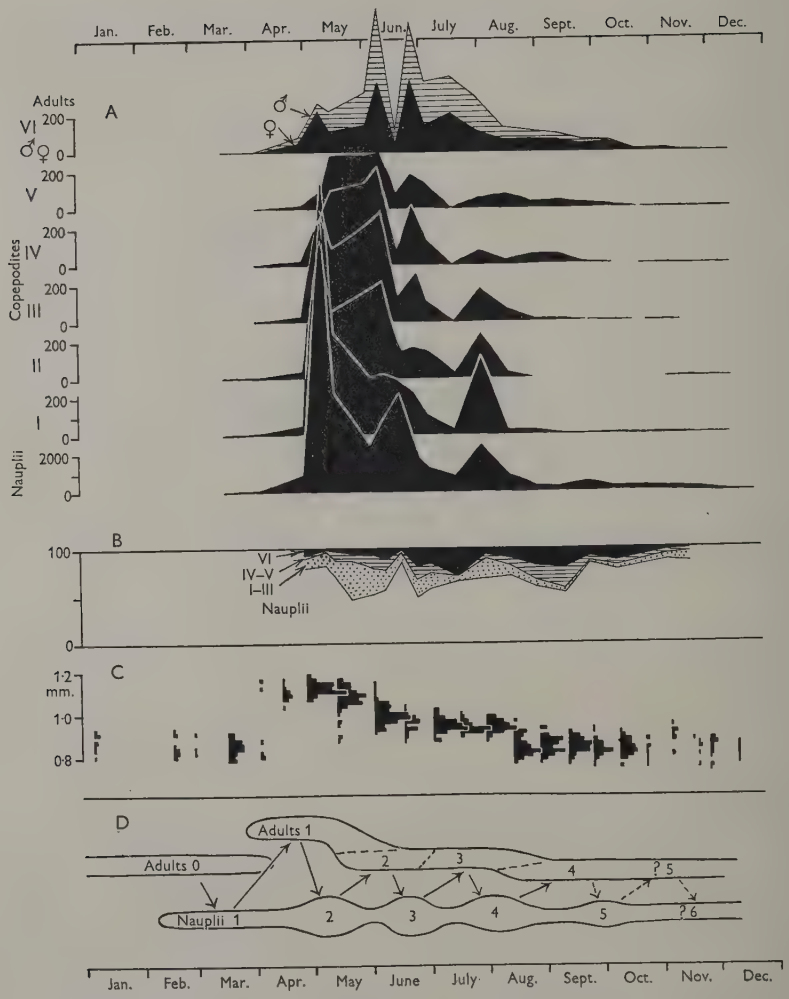

Fig. 6. *Acartia clausi*. A, abundance of stages; B, percentage distribution of stages; C, size-groups of adult females; D, interpretation.

Oithona similis (Fig 7, Table VII)

Abundant from April until October, with maxima in early May, late July and mid September.

There was again striking similarity to *Pseudocalanus*, but breeding was more diffuse. Generations can be traced as follows. Small adults '0' early in the year gave rise to nauplii, which developed to larger adults '1' in March, April and May. The nauplii '2' developed to adults '2', of smaller size, in June. The next group, adults '3', appeared in August and were smaller still. From here, the picture is obscure owing to continuous breeding with subsequent broods of adults appearing at the same size, but on the basis of the abundance and percentage graphs, together with comparison with other species, it would appear that adults occurring in September and October were adults '4' and those in November and December might be adults '5'.

Oithona nana (Fig. 8, Table VIII)

Abundant from September until December.

A few appeared early in the year, but were not counted. Those appearing after July were recorded and the nauplii counted. Nauplii appeared in August, and the first adults in considerable numbers in September. Inspection of the graphs reveals that probably a succession of generations occurred with adults in August, September, October, November and, it seems, in January when observations had ceased.

Oncaea venusta (Fig. 9, Table IX)

Abundant from September until December.

Oncaea was separated into copepodites and adults. As with *Oithona nana*, this species did not appear in numbers until August, after which it became plentiful. Separate generations were indicated coming to maturity in early September, September to October, November and possibly January. The numbers measured, although small, suggest size distinction between the generations.

Corycaeus anglicus (Fig. 10, Table IX)

Abundant from September until December.

Corycaeus anglicus was treated like *Oncaea* for similar reasons. It was similar to *Oithona nana* and *Oncaea* in its occurrence. Generations came to maturity in early September, and October to November. Another generation probably came to maturity in January, while the '0' group was possibly present in very small numbers in July. Separation of generations '2' and '3' was not possible on size.

Other Species

Calanus finmarchicus (Gunnerus) occurred in the samples, but in small numbers. As the last stages no doubt escaped the net, it was not counted.

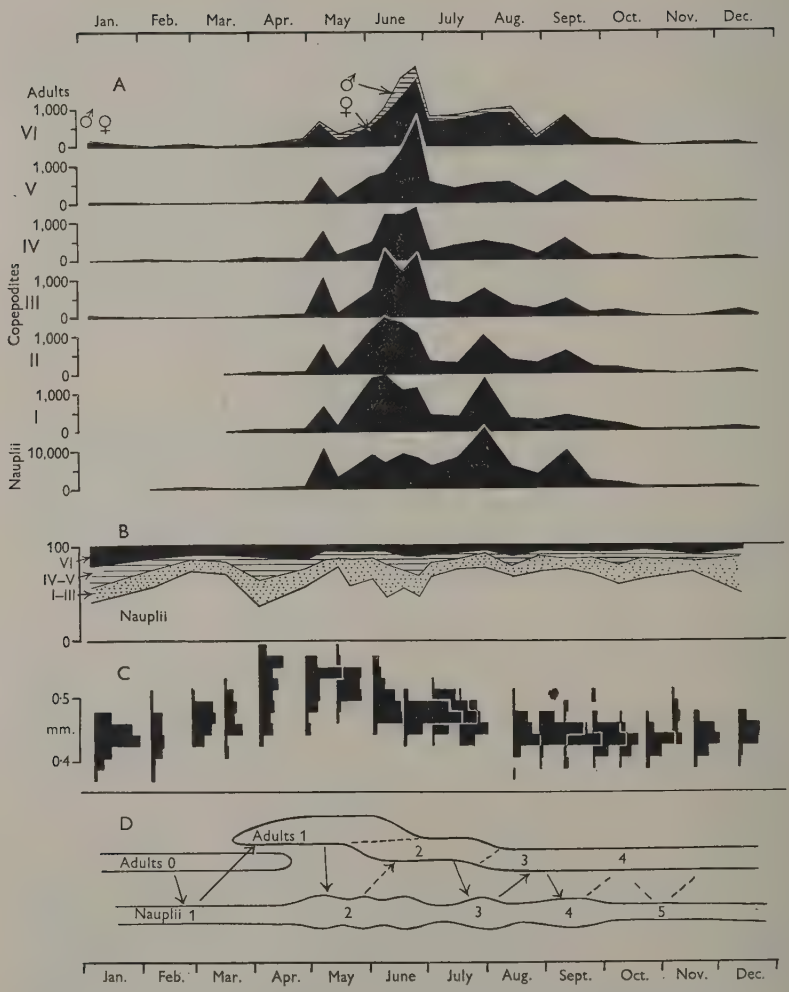

Fig. 7. *Oithona similis*. A, abundance of stages; B, percentage distribution of stages; C, size-groups of adult females; D, interpretation.

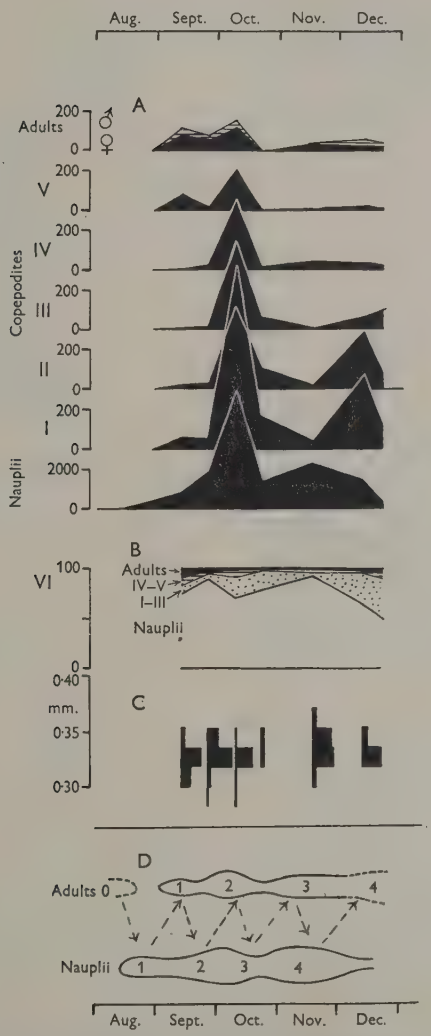

Fig. 8. *Oithona nana*. A, abundance of stages; B, percentage distribution of stages; C, size-groups of adult females; D, interpretation.

Centropages hamatus (Lilljeborg) occurred in small numbers in the summer months. Its appearance coincided with that of *C. typicus*. Owing to its small numbers, its nauplii were neglected and counted with those of *C. typicus*.

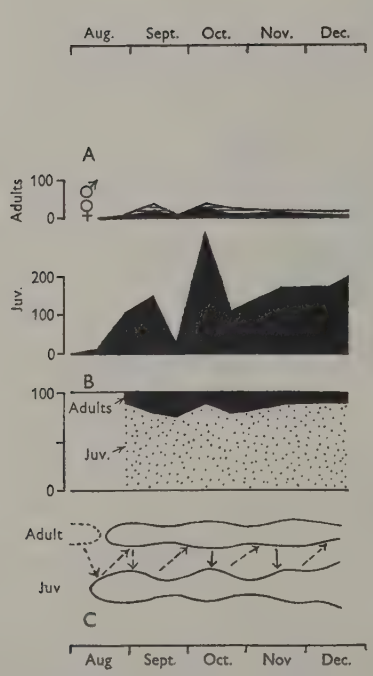

Fig. 9. *Oncaea venusta*. A, abundance of stages; B, percentage distribution of stages; C, interpretation.

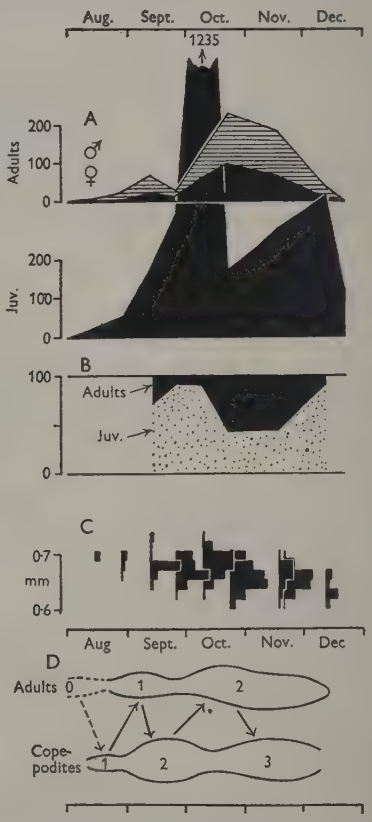

Fig. 10. *Corycaeus anglicus*. A, abundance of stages; B, percentage distribution of stages; C, size-groups of adult females; D, interpretation.

Euterpina acutifrons (Dana) occurred in the autumn at the same time as *Corycaeus* and *Oncaea*.

At the same time that the water was populated with *Oncaea*, *Corycaeus* and *Euterpina*, there appeared large numbers of nauplii of a type not previously encountered. These presumably belonged to these three species, and have been indicated as such in Fig. 13 (p. 414).

Size Near Plymouth

Pseudocalanus (Fig. 11, Table X) was present throughout the whole year. Sizes as a whole rose to a peak in April and then declined towards the end of the year. As in Loch Striven (Marshall, 1949) the adult female was larger than the adult male, and the Stage V female larger than the Stage V male, Stage IV being more nearly equal, with the female slightly larger until May, after which both sexes were about the same size.

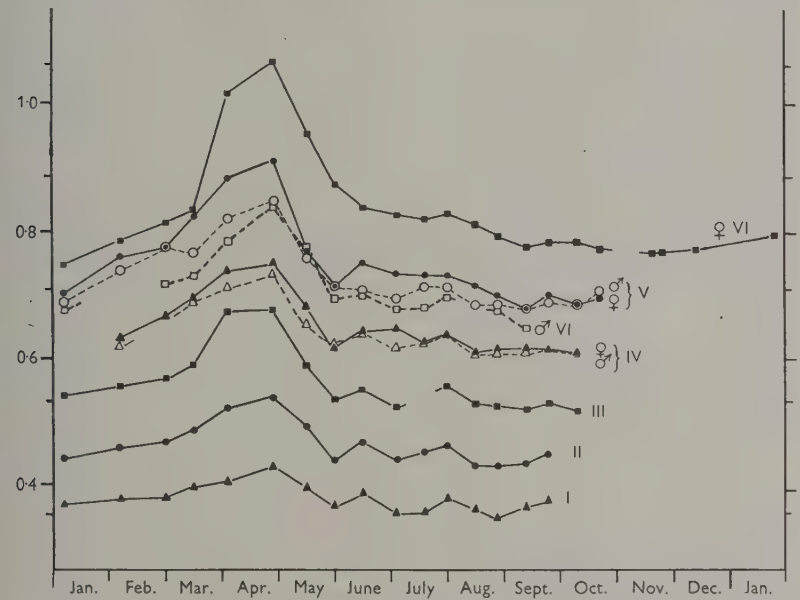

Fig. 11. *Pseudocalanus elongatus*. Median sizes of copepodites throughout the year

In Loch Striven, Marshall found that after May the male IV was slightly but distinctly larger than the female IV, while at Plymouth there appears to have been little difference. The only striking differences between the sizes at Plymouth and Loch Striven are that at Plymouth the median sizes of the IV, V and adult females were more widely separated than they were at Loch Striven, and no large variations in size of the Stage V occurred as did at Loch Striven. The changes in size of the adults were inadequate for separating broods at the end of the year.

Paracalanus was present (Table XI) throughout the whole year, and behaved in a similar manner to *Pseudocalanus*. Marshall found it present in numbers in Loch Striven only in the later part of the year. The relative sizes of the stages were similar to those found by Kraefft (1910) and Marshall (1949) in that the males of Stages IV, V and VI were larger than the corresponding female, the

male V being as large or larger than the adult female. The seasonal changes of size were similar to those of *Pseudocalanus*, but the adults differed in that the fluctuations in size from June to December were greater than those in *Pseudocalanus* and can be used with greater confidence for distinguishing the different generations. The increase in size of *Paracalanus* in October appears to have had no counterpart in *Pseudocalanus*.

In *Temora* (Table XIII), although few were measured, the sizes indicate the females IV, V and VI to have been larger than the corresponding males. A maximum size of adults occurred in May, followed by a sharp drop in size. Adults of small size occurred from July to September or October, with a minimum in September. This appears to have been about a month later than the corresponding minimum in Loch Striven. The fragmentary observations on sizes of the other stages indicate the seasonal changes to have been similar to those of the other species.

Acartia (Table XIV). As in *Temora*, the females IV, V and VI were larger than the corresponding males. The maximum size occurred in the latter half of April, as assumed by Marshall in Loch Striven, and thereafter sizes declined to a low size in August, September and October, to rise again in December and January.

In *Oithona similis* (Table XV) the sizes were very much as found by Marshall, with the exception that the adult female in the early part of the year was never smaller than the Stage V, although the sizes did become closely similar.

Oithona nana (Table XVI), *Oncaea* and *Corycaeus* (Table XVII) appeared in abundance from September to December, and in that time no changes occurred in the size of *Oithona nana*, while a slight decrease occurred in *Corycaeus*. *Oncaea* was not measured in sufficient numbers to enable conclusions to be drawn from size groups.

Distribution and Size in Adjacent Waters

The interpretation as to generations which has been placed on the changes observed at L 4 depends upon the changes being true changes with time, and not changes due to sampling different populations of copepods distributed in a localized manner in the water which passed Plymouth in the course of the year. In order to obtain information on the populations of copepods in adjacent waters, a few cruises were accomplished as follows:

January 1947—to the south-west of Plymouth and west of Penzance (Table XVIII).

June 1947—to the south-west of Plymouth (Table XIX).

August 1947—south and south-east of Plymouth (Table XX).

Hauls were made with a measuring net at the various stations and the samples were analysed to give numbers per cubic metre, and median sizes of adults.

In the January cruise, the noteworthy points were the existence of numbers of *Calanus finmarchicus* and *Metridia lucens*, at the stations off the coast of France and off Land's End, and the great increase in size of *Oithona* and *Pseudocalanus* off Land's End. The increased size might be suspected to have been due to a burst of phytoplankton during the previous November or December in this region. *Pseudocalanus* and *Paracalanus* were most abundant off the English coast and *Oithona* off the French coast.

In the June cruise, all species, with the exception of *Centropages hamatus* and *Calanus finmarchicus*, were most plentiful at stations 1–3. The size of *Pseudocalanus* was particularly great at station 4, at which it was least abundant. The figures for *Calanus* are probably low, as the large individuals no doubt escaped the net.

In the August cruise, the English side of the Channel seemed to be richer in all species except *Centropages typicus*, which was most common on the French side. The sizes of *Pseudocalanus* were similar with the exception of one station, no. 4, off Ushant, in which the median size was much higher than in the others. Again, it might be suspected that this marked the site of a transitory flowering of phytoplankton just at the time when these were coming to maturity.

In considering the significance of these regional variations, it would appear that, as far as these somewhat inadequate samples tell us, at most times a drift of water from 40 miles offshore over L4 would not unduly affect the general picture given of the total abundance of stock at these times. In some species such as *Temora*, however, the results might be seriously disturbed.

Discussion

Examination of the size-groups of adults has shown that a given group, appearing at a certain size, can be traced in subsequent samples until the members disappear. Meanwhile they are often replaced by other groups of adults appearing at a larger or smaller size. Thus while the median size can show a steady rise or fall, the size-groups can indicate a bimodal group with one population replacing another. When, as often, a new population, separable in the adults as being of different size, can be traced from the nauplii through the preceding samples, proof is offered that a new generation has arisen and that the change in size is not due to the sampling of different bodies of water. If the old brood of adults dies out slowly while the new brood is appearing, as in *Oithona*, the resulting median curve exhibits a gradual rise or fall, while if the new brood is produced suddenly in superior numbers, as in *Temora*, the curve will be step-like in form. The size-groups for *Pseudocalanus*, Stages I–III and females IV–VI, are given in Fig. 12. These show that although the adults may form bimodal groups, the younger stages rarely do so. This is because, although the adults may survive for a considerable time at a given

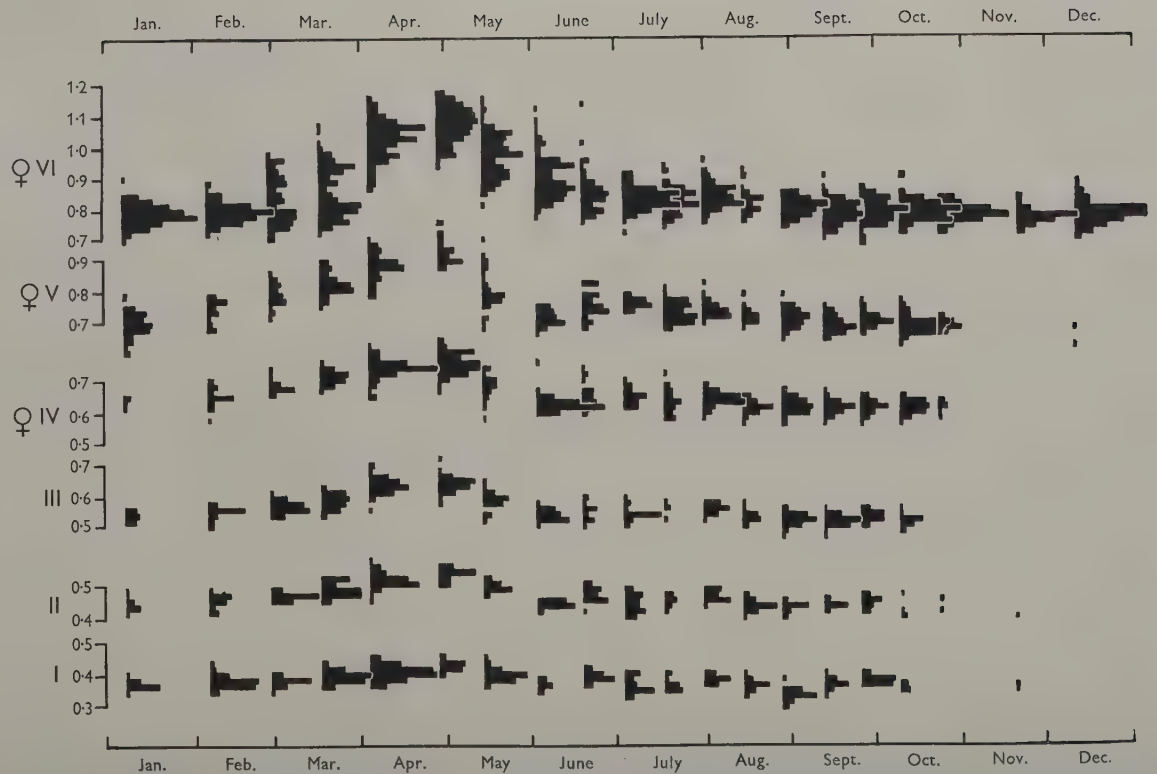

Fig. 12. *Pseudocalanus elongatus*. Size-groups of copepodites I–III and females IV–VI.

size, the developmental stages are transitory. The sizes of the adults are the result of the varied conditions for possibly some weeks preceding sampling; not to exclude the effect of the size of the previous stages, as suggested by Ussing (1938). The sizes of the younger developmental stages are a reflexion of conditions immediately preceding sampling, and bimodal groups exist only if conditions change very rapidly. It is noteworthy that all the stages change size in unison. Ussing (1938) obtained evidence to show that in Greenland the size of *Calanus* was partly dependent upon the size of the preceding stage, and partly on the state of nutrition before moulting. If that were so at Plymouth it would be evident from a rise in size, of, say, Stages I or II being followed by a rise of Stages IV or V in the next sample 2 weeks later. The absence of this effect may be due to the surplus of food which we know to be available (Harvey *et al.*, 1935) in Plymouth waters. The total densities per cubic metre of the various species of copepods throughout the year are illustrated in Fig. 13. All have been drawn to the same scale. Copepods are marked solid black, the nauplii are added as a continuous line and the eggs as dotted line. No nauplii are indicated for *Oncaea* and *Corycaeus*, but the group of nauplii belonging to these two species and to *Euterpina* is figured separately.

The totals indicated here represent the majority of specimens present in the plankton off Plymouth, for *Calanus finmarchicus*, although representing on occasions a large part of the plankton by bulk, was numerically poor compared with these smaller species.

The appearance of the graphs for *Paracalanus* indicates a delay of about 3 weeks in the development of the generation at the end of June. Attention was drawn to it in the interpretation for *Paracalanus* (Fig. 3). It can also be seen in *Temora*. It would be expected that if this was due to poor phytoplankton, this effect would be visible in all the species. But this was not so. In *Pseudocalanus*, *Acartia* and *Oithona*, there was a repetition at the end of June of the conditions $2\frac{1}{2}$ weeks earlier, evident as a bimodal peak of abundance of adults and late stages in *Pseudocalanus* and *Acartia*, and of early stages in *Oithona*, and as a lengthened peak of abundance of adults in *Oithona*. Fish (1936*a*, *b*), found a difference in the stage of development of a population according to the time of flowering of the spring phytoplankton. It might be expected that a similar phenomenon might be encountered in these waters. The effects noted above would be entirely in accord with the drifting over L4 in mid-June of water in which the spring increases had set in some $2\frac{1}{2}$ weeks earlier. Over the whole year, the water was characterized by *Sagitta setosa* (Mr. P. G. Corbin, personal communication).

The occurrence of the various species has been summarized by Marshall (1949) and reference may be made to that paper for comparison. The course of generations in Loch Striven and at Plymouth would appear to be similar in very broad outline. The time of development from nauplius to adult in the different species can be seen to range from about 4 to 6 weeks, while the periods

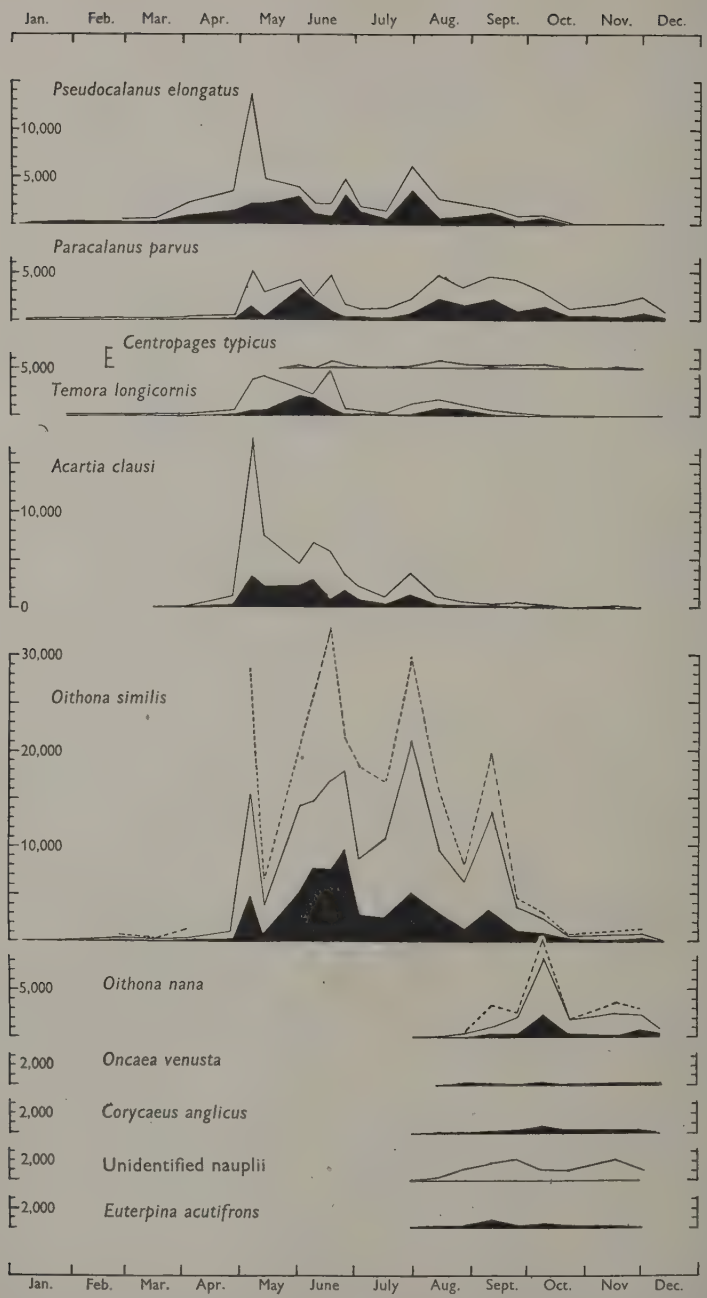

Fig. 13. Numbers per cubic metre of the smaller copepods throughout the year, all to same scale. Solid black, copepodites and adults. Continuous line, all stages including nauplii. Dotted line, total plus eggs.

between successive broods of adults were from 6 weeks to 2 months. These results are therefore closely comparable to those of Fish (1936*a*, *b*) who found generations of *Pseudocalanus* and *Oithona* in the Gulf of Maine to occur with the same developmental periods.

There was a great similarity in the behaviour of the different species, as found also by Marshall (1949) in Loch Striven.

It may be possible that the dynamic relationships which exist between the phytoplankton and the zooplankton serve to keep the generations of the different species more or less in step, as the conditions which cause the production of a good brood of nauplii in general appear to affect all the species alike. Thus it may well be that these species may have quite different development times if reared in the laboratory, whereas in the sea their generations appear to keep in step. Laboratory work on the factors relating phytoplankton and copepod populations is needed to elucidate these processes, and to give the final answer concerning the development time in species which breed continuously in the sea.

Summary

The life histories of the small planktonic copepods of Plymouth were studied during 1947. The samples were taken at Station L4 with Harvey measuring nets, and are thus truly quantitative.

The main species concerned were *Pseudocalanus elongatus*, *Paracalanus parvus*, *Centropages typicus*, *Temora longicornis*, *Acartia clausi*, *Oithona similis*, *O. nana*, *Oncaea venusta* and *Corycaeus anglicus*.

The species common in summer—all but the last three of the above—behaved in a very similar way, producing probably five generations in the course of the year, but differing from each other in the relative and absolute abundance of the different stages at different times of the year.

The species restricted to autumn and winter—*Oithona nana*, *Oncaea* and *Corycaeus*—resembled each other in appearing in countable numbers as nauplii in August and producing three broods in the late months of the year.

The Stages I–VI of the various species were measured throughout the year, and the variations in size found to be similar to those of the copepods of Loch Striven as found by Marshall.

The distribution of copepods in adjacent waters during January, June and August were investigated. It is concluded that a drift of water from the south-west of up to 40 miles would be unlikely to disturb severely the picture of the seasonal variations in total numbers of the copepod population as obtained from samples taken at L4.

The observed changes in size and abundance are discussed, with reference to possible water movements.

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APPENDIX

Table I. Stations, Temperature and Degree of Subsampling

Date	Station	Temperatures 1 m.	Temperatures 30 m.	Water fished (litres)	Volumes examined for various stages (litres): *Pseudocalanus*	*Paracalanus*	*Centropages*	*Temora*	*Acartia*	*Oithona similis*	*O. nana*	*Oncaea*	*Corycaeus*	*Euterpina*	Unidentified nauplii
6. i. 47	L 4	..	..	437	437 with all species										
5. ii	L 4	7·4	7·4	2760	1000 with all species										
17. ii	L 4	6·0	6·2	..											
27. ii	L 4	5·57	5·59	2350	1000 with all species										
7. iii	L 4	6·10	6·12	..											
12. iii	L 4	5·55	5·55	..											
17. iii	L 4	6·04	6·00	1900	N. 1000, I–IV 1500. All species										
28. iii	L 4	7·2	7·2	..											
3. iv	L 4	8·2	7·4	1950	N. 400 I–III 1000 IV–VI 1500	N. 400 I–III 1000 IV–VI 2000	N. 400 I–VI 1000	N. 400 I–III 1000 IV–VI 2000	..	..	..	..	..	..	..
8. iv	L 4	8·0	7·7	..											
15. iv	L 4	9·51	7·76	..											
28. iv	L 4	9·35 (surface)	8·43	2250	N. 200 I–VI 400 } with all species										
8. v	3½ miles outside breakwater	10·3	..	604	N. 25 I–VI 50 } with all species										
14. v	2 miles outside breakwater	11·2 (1 m.)	..	332	N. 50 I–VI 300 } with all species										
2. vi	L 4	12·27	10·52	2250	N. 100 I–VI 100 } with all species except adults of *Temora*, *Centropages*, *Acartia* (600)										
9. vi	L 4	11·40	10·81	2030	501 with all species										
18. vi	L 4	12·75	..	625	N. 50 I–V 250 VI 500	N. 50 I–V 250 VI 500	N. 50 I–III 250 IV–VI 500	N. 50 I–IV 250 V–VI 500	N. 50 I–IV 250 V–VI 500	50	50	..	..	..	..
26. vi	L 4	14·00	11·64	1800	N. 50 I–VI 100	N. 50 I–VI 100	N. 50 I–VI 100	N. 50 I–III IV–VI 250	N. 50 I–VI 100	50	..	..	..	..	..
3. vii	L 4	16·62	11·79	1650	N. 100 I–VI 500 } with all except *Oithona* (100)										
17. vii	L 4	14·90	11·50	1300	N. 100 I–III 250 IV–VI 1050	N. 100 I–IV 250 V–VI 1050	N. 100 I–III 250 IV–VI 1050	N. 100 I–II 250 III–VI 1050	N. 100 I–II 250 III–V 1050 VI 450	N. 50 I–II 100 III–VI 250	400	200	..	..	..
24. vii	L 4	15·00	12·95	..											
31. vii	L 4	16·82	13·13	900	N. 50 I–VI 200	N. 50 I–VI 200	N. 50 I–II 200 III–VI 500	N. 50 I–III 200 IV–VI 500	N. 50 I–III 200 IV–VI 500	N. 50 I–III 50 IV–VI 200	50	..	..	..	..

5. viii	L 4	16·33	14·70	..	..	..	..	..	..	..	..	..	..	..
14. viii	L 4	16·86	15·39	1480	N. 100 I–II 200 III–VI 1000	N. 100 I–III 200 IV–VI 1000	N. 100 I–III 200 IV–VI 1000	N. 100 I–III 200 IV–VI 1000	N. 100 I–VI 200	N. 100 I–VI 200	100	Juv. 200	Juv. 200 Adults 1000	1000	100
19. viii	L 4	18·43	14·30	..	..	..	..	..	..	..	..	..	..	..	..
28. viii	L 4	17·14	16·42	1800	N. 200 I–II 200 III 500 IV–VI 1000	N. 200 I–III 200 IV 500 V, VI 1000	N. 200 I–II 200 III–VI 1000	N. 200 I–II 200 III 500 IV–VI 1000	N. 200 I–II 200 III–VI 1000	N. 200 I–IV 200 V–VI 500	200	Juv. 200	500	200	200
4. ix	L 4	16·99	16·60	..											
12. ix	L 4	17·50	16·01	1550	N. 100 I–III 200 IV–VI 1000	N. 100 I–IV 200 V–VI 1000	N. 100 I–III 200 IV–VI 1000	N. 100 I–III 200 IV–VI 1000	N. 100 I–III 200 IV–VI 1000	N. 100 I–VI 200	N. 100 I–IV 200	200	Juv. 200 Adults 1000	200	100
17. ix	L 4	16·70	15·65	..	..	..	..	..	..	..	..	..	..	..	..
25. ix	L 4	15·90	15·85	1210	N. 200 I–III 500 IV–VI 1000	N. 200 I–IV 500 V–VI 1000	N. 200 I–IV 500 V–VI 1000	N. 200 I–VI 1000	N. 200 I–II 500 III–VI 1000	N. 150 I 200 II–VI 500	N. 200 I–II 200 III–VI 500	Juv. 500 Adults 1000	Juv. 200 Adults 1000	500	50 50
2. x	L 4	15·65	15·10	..	..	..	..	..	..	..	..	..	..	..	..
9. x	L 4	15·45	15·39	1520	N. 200 I–II 200 III–VI 1000	N. 200 I–II 200 III–IV 500 V–VI 1000	N. 200 I–II 500 III–VI 1000	N. 200 I–II 200 III–VI 1000	N. 200 I 200 II–III 500 IV–VI 1000	N. 200 I–IV 200 V–VI 500	N. 150 I–VI 200	200	Juv. 200 Adults 1000	200	50
15. x	L 4	15·59	15·54	..	..	..	..	..	..	..	..	..	..	..	..
23. x	L 4	15·35	15·38	1400	N. 250 I–III 500 IV–VI 1000	N. 250 I–III 500 IV–VI 1000	N. 250 I–III 500 IV–VI 1000	N. 500 I–III 500 IV–VI 500	N. 250 I–III 500 IV–VI 1000	N. 250 I–III 500 IV–VI 1000	N. 100 I–III 500 IV–VI 1000	500	Juv. 500 Adults 1000	500	50
28. x	L 4	14·89	14·90	..	..	..	..	..	..	..	..	..	..	..	..
6. xi	1 mile outside breakwater	13·8 (surface)	..	..	..	..	..	..	..	..	..	..	..	..	..
17. xi	L 4	13·78 (1 m.)	13·79	3140	N. 500 I–III 500 IV–VI 1000	N. 500 I–IV 500 V–VI 1000	N. 500	N. 500	N. 500 I–III 500 IV–VI 1000	N. 500 I–VI 500	N. 500 I–VI 500	500	Juv. 500 Adults 1000	500	500
26. xi	L 4	13·35	13·36	..	..	..	..	..	..	..	..	..	..	..	..
11. xii	L 4	11·97	12·00	2740	N. 200 IV–VI 2500	N. 200 IV–VI 1000	N. 200	N. 200	N. 200 I–VI 1000	N. 200 I–VI 200	N. 200 I–VI 200	Juv. 200 Adults 1000	Juv. 200 Adults 1000	200	200
22. xii	L 4	11·40	11·65	2540	N. 200 I–III 200 IV–VI 1000	N. 200 I–III 200 IV–VI 1000	N. 200	N. 200	N. 200	N. 200 I–VI 200	N. 200 I–VI 200	200	200		
7. i. 48	L 4	10·32	10·40	..	..	..	..	..	..	..	..	..	..	..	..
16. i	L 4	10·00	10·62	..	..	..	..	..	..	..	..	..	..	..	..
13. ii	L 4	9·80	9·82	..	..	..	..	..	..	..	..	..	..	..	..
19. ii	L 4	9·29	9·29	..	..	..	..	..	..	..	..	..	..	..	..

Note. N. is used as abbreviation for nauplii; and Roman numerals for copepodite stages.

Table II. *Pseudocalanus elongatus*. Abundance

	Number per cubic metre									Percentages			
Date	Nauplii	I	II	III	IV	V	VI♀	VI♂	Total	N.	I–III	IV–V	VI
6. i	220	18	16	14	14	62	66	7	417	53·8	9·0	12·3	24·9
5. ii	166	47	20	23	36	30	57	3	382	71·3	12·8	9·4	6·5
27. ii	349	34	21	23	19	34	63	8	551	62·6	15·0	9·6	12·8
17. iii	357	69	38	22	20	43	35	15	601	59·4	21·4	10·8	8·3
3. iv	1,348	182	112	181	147	108	126	76	2280	59·0	20·8	11·2	8·8
28. iv	2,145	125	130	398	341	178	120	68	3,505	61·5	18·7	14·8	5·3
8. v	11,440	280	220	600	380	440	120	120	13,600	83·8	8·1	6·0	1·8
14. v	7,720	1,180	110	93	144	230	270	193	9,940	77·5	14·0	3·8	4·6
22. v	..	..	..	..	..	..	..	..	..	49·7	39·8	6·4	4·0
2. vi	858	102	249	895	784	572	277	74	3,811	22·5	32·7	35·6	9·2
9. vi	940	..	40	140	100	320	440	80	2,060	45·6	8·7	20·4	25·2
18. vi	1,260	212	92	60	64	108	218	80	2,094	62·2	17·4	8·2	14·4
26. vi	1,680	180	260	780	750	610	330	130	4,720	35·6	25·8	28·8	9·1
3. vii	1,150	152	70	60	80	156	224	98	1,990	57·7	14·2	11·9	16·3
7. vii	830	56	36	16	33	80	287	91	1,429	58·2	7·6	7·9	26·5
31. vii	2,500	620	635	600	740	495	350	70	6,010	41·7	30·9	20·5	7·0
14. viii	2,060	155	175	139	94	42	32	8	2,705	76·1	17·7	5·0	1·5
28. viii	1,325	130	80	70	163	195	155	89	2,184	60·7	12·8	15·3	11·2
12. ix	570	255	205	270	262	115	75	11	1,773	32·1	41·2	21·8	4·8
25. ix	340	54	34	84	148	74	34	4	772	44·0	22·3	28·7	4·9
9. x	215	15	15	39	257	287	94	8	930	23·1	7·4	58·5	11·0
23. x	20	..	4	..	10	31	23	2	90	22·2	4·4	45·5	27·8
17. xi	10	..	..	..	1	5	1	..	17	..	..	..	..
11. xii	100	..	..	..	1	4	10	1	115	..	..	..	..
22. xii	130	10	..	..	..	..	..	..	140	..	..	..	..

Table III. *Paracalanus parvus*. Abundance.

	Number per cubic metre									Percentages			
Date	Nauplii	I	II	III	IV	V	VI♀	VI♂	Total	N.	I–III	IV–V	VI
6. i	..	2	55	62	41	41	69	7	121	24·1	43·6	20·6	11·7
5. ii	..	26	33	24	30	28	22	..	173	35·4	38·6	20·7	5·2
27. ii	128	7	3	16	21	21	25	1	222	57·7	12·0	19·0	11·3
17. iii	95	18	4	2	4	20	18	..	161	59·0	14·9	14·9	11·2
3. iv	208	25	18	12	18	8	12	2	303	68·6	18·1	8·6	4·6
28. iv	345	48	23	28	28	13	15	..	500	69·0	19·8	8·2	3·0
8. v	3760	400	240	100	120	360	160	40	5180	72·5	14·3	9·3	3·9
14. v	2460	170	37	57	47	30	83	17	2901	84·9	9·1	2·6	3·5
22. v	..	..	..	..	..	..	..	..	..	19·5	64·8	12·8	2·8
2. vi	636	55	166	1540	1226	332	74	..	4029	15·8	43·6	38·6	1·8
9. vi	240	..	80	80	840	820	400	20	2480	9·7	6·4	66·9	16·9
18. vi	3840	276	80	72	124	120	218	28	4758	80·6	9·0	5·1	5·2
26. vi	1300	70	70	30	40	10	140	..	1660	78·3	10·2	3·0	8·4
3. vii	700	18	26	66	70	60	62	22	1024	68·3	10·7	12·7	8·2
7. vii	940	24	4	..	..	12	65	13	1058	89·0	2·6	1·1	7·4
31. vii	1540	110	120	65	135	125	180	..	2275	67·7	13·0	11·4	7·9
14. viii	2360	415	390	370	354	372	232	53	4546	51·9	25·8	16·0	6·3
28. viii	2025	335	240	160	230	201	227	42	3460	58·5	21·2	12·4	7·8
12. ix	2350	230	320	355	760	300	236	19	4570	51·4	19·8	23·2	5·6
25. ix	3270	276	160	136	124	89	125	6	4186	78·1	13·7	5·1	3·1
9. x	1460	270	235	372	260	195	77	18	2887	50·6	30·4	15·8	3·3
23. x	544	180	106	56	30	43	43	4	1006	54·1	34·0	7·3	4·7
17. xi	1294	130	82	32	42	29	58	2	1669	77·5	14·6	4·3	3·6
11. xii	1570	285	275	105	44	39	34	2	2354	66·7	28·2	3·5	1·5
22. xii	645	160	20	15	8	3	2	..	853	75·6	22·8	1·3	0·2

TABLE IV. *CENTROPAGES TYPICUS*. ABUNDANCE

	Number per cubic metre								
Date	Nauplii	I	II	III	IV	V	VI♀	VI♂	Total
6. i	..	..	..	..	..	..	2	..	2
5. ii	8	..	..	..	..	..	..	..	8
27. ii	7	..	..	..	..	..	..	..	7
17. iii	7	..	..	..	1	..	..	..	8
3. iv	14	..	1	..	..	..	2	..	17
28. iv	10	..	..	..	..	..	..	..	10
8. v	..	..	..	..	..	..	..	..	..
14. v	..	..	..	..	..	3	3	..	6
2. vi	230	10	..	..	10	..	2	1	253
9. vi	20	..	..	..	..	..	..	..	20
18. vi	640	16	32	44	14	10	..	2	758
26. vi	220	..	10	20	10	10	..	10	280
3. vii	40	8	10	2	2	4	12	12	90
7. vii	80	5	..	..	2	3	1	6	97
31. vii	220	..	5	6	18	36	6	6	297
14. viii	830	..	..	..	3	3	5	4	845
28. viii	440	..	..	4	7	5	5	2	463
12. ix	920	..	10	35	79	46	18	24	1132
25. ix	360	..	2	2	..	3	1	1	368
9. x	315	22	18	2	5	2	..	..	364
23. x	12	..	..	..	1	..	..	..	13
17. xi	90	..	..	..	..	..	..	..	90
11. xii	10	..	..	..	..	..	..	..	10
22. xii	..	..	..	..	..	..	..	..	..

TABLE V. *TEMORA LONGICORNIS*. ABUNDANCE

	Number per cubic metre									Percentages			
Date	Nauplii	I	I	III	IV	V	VI♀	VI♂	Total	N.	I–III	IV–V	VI
6. i	16	..	2	2	..	..	..	..	20	..	..	..	..
5. ii	54	2	..	1	..	1	..	..	58	96·4	2·4	0·6	0·6
27. ii	74	2	1	1	..	..	1	..	79	93·4	5·7	..	0·9
17. iii	82	11	2	..	2	..	1	..	98	83·8	13·3	2·0	1·0
3. iv	68	6	6	3	5	4	1	2	95	71·5	15·8	9·5	3·2
28. iv	455	3	23	25	10	23	13	5	557	81·6	9·2	5·9	3·2
8. v	3400	240	160	40	40	20	20	..	3920	86·7	11·2	1·5	0·5
14. v	3600	300	77	23	37	27	27	17	4108	87·7	9·7	1·6	1·1
22. v	..	..	..	..	..	..	..	..	..	36·2	56·9	5·8	1·0
2. vi	729	194	507	747	295	147	115	158	2892	25·2	50·0	15·3	9·5
9. vi	320	80	120	40	860	520	160	180	2280	14·0	10·5	60·5	14·9
18. vi	3840	356	196	56	32	6	24	32	4542	84·6	13·4	0·8	1·2
26. vi	440	30	..	..	24	28	48	96	666	66·1	4·5	7·8	21·6
3. vii	260	22	38	48	54	54	40	36	552	47·1	19·6	19·6	13·8
7. vii	40	4	..	1	1	21	65	75	207	19·6	2·4	10·6	67·6
31. vii	940	70	40	10	..	8	18	24	1110	84·7	10·8	0·7	3·8
14. viii	980	250	115	165	97	57	7	10	1681	58·3	31·5	9·2	1·0
28. viii	505	80	60	88	214	144	48	42	1181	42·8	19·3	30·3	7·6
12. ix	340	40	15	35	25	21	17	34	527	64·5	17·1	8·7	9·7
25. ix	185	15	10	6	6	4	3	5	234	79·0	13·2	4·3	3·4
9. x	60	..	5	2	1	2	3	3	76	78·9	9·2	3·9	7·9
23. x	16	4	..	..	..	..	1	..	21	..	..	..	..
17. xi	32	..	..	..	..	..	..	..	32	..	..	..	..
11. xii	45	..	..	..	..	..	..	..	45	..	..	..	..
22. xii	10	..	..	..	..	..	..	..	10	..	..	..	..

TABLE VI. *ACARTIA CLAUSI*. ABUNDANCE

	Number per cubic metre									Percentages			
Date	Nauplii	I	II	III	IV	V	VI♀	VI♂	Total	N.	I–III	IV–V	VI
6. i	..	..	..	..	..	..	5	..	5	..	..	..	..
5. ii	..	..	..	1	2	2	1	..	6	..	..	..	..
27. ii	25	..	..	..	..	..	..	..	25	..	..	..	..
17. iii	23	..	1	1	1	1	3	..	30	..	..	..	..
3. iv	45	7	8	2	3	3	3	1	72	..	..	..	..
28. iv	875	48	40	28	23	18	45	33	1,110	79·0	10·4	3·7	7·0
8. v	14,280	1,340	740	580	240	100	220	40	17,540	81·2	15·2	1·9	1·5
14. v	5,320	547	353	390	394	287	110	107	7,508	70·7	17·2	9·1	2·9
22. v	..	..	..	..	..	..	..	..	..	45·9	38·4	9·8	5·9
2. vi	2,350	304	461	516	434	286	141	173	4,665	50·4	27·5	15·4	6·7
9. vi	3,800	320	520	580	520	300	360	400	6,800	55·9	20·9	12·0	11·2
18. vi	5,060	288	144	136	72	84	44	70	5,898	86·9	9·6	2·6	1·9
26. vi	1,740	230	170	260	310	100	380	310	3,508	48·6	18·4	13·7	19·3
3. vii	1,290	108	146	108	132	82	142	230	2,238	57·7	16·4	9·6	16·6
7. vii	880	28	28	6	5	2	204	193	1,346	65·5	4·6	0·5	29·5
31. vii	2,460	410	240	170	78	56	180	174	3,696	66·9	21·6	3·6	7·7
14. viii	830	25	35	70	25	75	60	65	1,185	70·0	11·0	8·4	10·5
28. viii	335	25	..	19	56	31	62	46	574	58·4	7·7	15·1	18·9
12. ix	230	5	..	15	57	39	58	32	436	52·6	4·6	22·0	20·6
25. ix	505	6	2	2	12	25	34	18	604	83·6	1·6	6·1	8·6
9. x	285	10	6	2	7	12	46	5	373	76·4	4·8	5·1	13·7
23. x	..	8	4	..	..	..	4	..	16	..	..	..	..
17. xi	218	12	10	2	7	3	1	3	256	85·1	9·4	3·9	1·6
11. xii	10	2	4	1	..	..	..	..	17	..	..	..	..
22. xii	..	..	..	..	..	..	..	..	..	..	..	..	..

TABLE VII. *OITHONA SIMILIS*. ABUNDANCE

Date	Number per cubic metre: Eggs	Nauplii	I	II	III	IV	V	VI ♀	VI ♂	Total excl. eggs	Percentages: N.	I–III	IV–V	VI	Eggs per egg-sac
6. i	Lost through		9	16	30	18	66	156	27	..	40·9	15·9	22·6	20·9	..
5. ii	net mesh		9	15	27	27	24	29	3	..	57·1	17·9	12·2	12·8	..
27. ii	272	254	19	9	12	6	11	28	52	451	74·0	11·5	5·0	9·5	6·3
17. iii	80	156	16	8	4	8	8	22	2	224	69·7	12·5	7·1	10·7	8·9
3. iv	835	183	39	48	43	57	64	45	14	493	37·2	26·4	24·6	12·0	12·8
28. iv	?	630	80	63	63	45	55	140	25	1,101	57·0	18·7	9·1	14·9	..
8. v	13,240	10,560	700	800	1,040	740	720	580	130	15,320	68·8	16·6	9·5	5·0	13·8
14. v	2,780	3,000	130	130	103	130	157	147	50	3,847	78·0	9·4	7·4	5·1	13·9
22. v	..	..	..	..	..	..	..	..	..	..	58·0	28·2	7·9	5·8	..
2. vi	5,750	8,990	1,410	1,190	728	434	701	508	101	14,062	64·0	23·8	8·1	4·9	9·7
9. vi	10,280	6,960	1,500	1,480	1,760	1,200	820	780	180	14,680	47·4	32·3	13·8	6·5	10·1
18 vi	15,920	9,320	1,100	1,340	720	1,200	1,380	1,320	480	16,860	55·4	18·7	15·3	10·7	11·7
26. vi	3,720	8,280	1,140	1,040	1,680	1,400	2,180	1,760	340	17,820	46·5	21·7	20·1	11·8	8·8
3. vii	9,650	5,840	440	360	430	260	550	630	140	8,650	67·5	14·2	9·4	8·9	11·8
7. vii	6,240	8,040	390	300	344	408	408	672	128	10,690	75·2	9·7	7·6	7·5	7·4
31. vii	8,540	16,040	1,400	1,020	740	525	510	865	82	21,182	76·2	14·9	4·9	4·4	8·4
14. viii	7,460	6,050	355	370	305	395	525	895	155	9,050	66·8	11·4	10·2	11·6	6·7
28. viii	2,900	3,850	295	295	225	155	164	218	40	5,242	73·4	15·5	6·1	4·9	7·4
12. ix	6,230	10,170	450	605	470	540	545	735	35	13,550	75·0	11·2	8·0	5·7	6·8
25. ix	1,060	2,454	285	198	124	102	142	206	14	3,529	69·5	17·2	6·9	6·3	7·1
9. x	680	1,400	170	155	145	165	162	138	13	2,348	59·6	20·0	13·9	6·4	8·0
23. x	128	396	54	48	32	24	35	24	1	614	64·4	31·8	9·6	4·1	6·4
17. xi	398	460	36	18	22	28	20	56	10	650	70·7	11·7	7·4	10·2	8·0
11. xii	485	480	115	95	145	55	30	55	..	975	49·2	36·4	8·7	5·6	6·9
22. xii	..	50	30	20	30	5	10	10	..	155	..	..	..	..	..

TABLE VIII. *OITHONA NANA*. ABUNDANCE

Date	Number per cubic metre: Eggs	Nauplii	I	II	III	IV	V	VI ♀	VI ♂	Total excl. eggs	Percentages: N.	I–III	IV–V	VI	Eggs per egg-sac
31. vii	..	..	40	..	..	..	..	..	..	40	..	..	..	..	..
14. viii	..	40	20	10	..	..	..	10	..	80	..	..	..	..	..
28. viii	..	415	..	..	..	..	..	..	..	415	..	..	..	..	..
12. ix	2120	910	65	25	10	10	85	80	35	1220	74·6	8·2	7·8	9·4	15·1
25. ix	410	1910	60	35	20	30	22	60	14	2137	89·5	5·4	2·4	2·8	13·7
9. x	1900	5870	915	410	435	345	210	120	35	8310	70·6	21·2	6·7	1·5	15·2
23. x	..	1480	174	118	66	24	11	4	..	1887	78·8	19·1	1·9	0·2	..
17. xi	1144	2318	48	20	14	50	12	32	2	2506	92·5	3·3	2·9	1·4	16·8
11. xii	375	1555	370	295	70	40	30	30	30	2420	64·2	30·4	2·9	2·5	10·7
22. xii	..	415	140	90	105	30	15	25	15	835	49·6	40·1	5·4	4·8	..

TABLE IX. *ONCAEA VENUSTA*, *CORYCAEUS ANGLICUS*, *EUTERPINA ACUTIFRONS* AND UNIDENTIFIED NAUPLII. ABUNDANCE

Date	*Oncaea venusta*: No. per cu.m. Juv.	♀	♂	Total	Percentage: Juv.	Adult	*Corycaeus anglicus*: No. per cu.m. Juv.	♀	♂	Total	*Euterpina acutifrons*: Percentage: Juv.	Adult	No. per cu.m.	Unidentified nauplii No. per cu.m.
31. vii	..	..	..	..	..	..	..	..	..	..	..	..	20	..
14. viii	15	..	..	15	..	..	25	3	3	31	..	..	119	340
28. viii	105	..	10	115	91·2	8·8	55	6	20	81	..	..	278	1115
12. ix	150	20	20	190	79·0	21·0	180	25	44	249	72·3	27·7	905	1640
25. ix	28	3	5	36	77·8	22·2	325	13	15	353	92·3	7·9	292	2140
9. x	315	30	10	355	88·8	11·2	1235	63	73	1371	90·1	9·9	490	1220
23. x	114	10	18	142	80·2	19·8	176	98	133	407	43·2	56·7	232	1080
17. xi	172	16	6	194	88·5	11·4	284	69	115	326	43·5	56·5	234	2200
11. xii	175	7	15	197	88·5	11·4	365	12	26	403	90·6	9·4	18	1040
22. xii	200	5	15	220	90·8	9·2	110	..	..	110	100·0	..	..	..

Table X. *Pseudocalanus elongatus*. Size in mm.

Stage	Date	No.	0·442–0·495	0·495–0·548	0·548–0·602	0·602–0·655	0·655–0·708	0·708–0·761	0·761–0·813	0·813–0·867	0·867–0·920	0·920–0·973	0·973–1·03	1·03–1·08	1·08–1·13	1·13–1·18	Median size
VI ♂	6. i	16	..	..	..	4	9	1	2	..	..	..	..	..	..	..	0·673
	5. ii	3	..	..	..	2	1	..	..	..	..	..	..	..	..	..	..
	27. ii	10	..	..	..	..	3	5	2	..	..	..	..	..	..	..	0·717
	17. iii	48	..	..	..	1	11	30	6	..	..	..	..	..	..	..	0·728
	3. iv	78	..	..	..	..	3	18	52	5	..	..	..	..	..	..	0·786
	28. iv	26	..	..	..	..	..	..	5	18	3	..	..	..	..	..	0·837
	14. v	64	..	..	..	..	3	22	32	6	1	..	..	..	..	..	0·773
	2. vi	17	..	..	..	1	11	4	..	..	1	..	..	..	..	..	0·692
	18. vi	27	..	..	..	..	20	4	3	..	..	..	..	..	..	..	0·699
	3. vii	47	..	..	..	11	25	11	..	..	..	..	..	..	..	..	0·678
	17. vii	95	..	..	..	11	73	10	1	..	..	..	..	..	..	..	0·679
	31. vii	14	..	..	..	..	10	4	..	..	..	..	..	..	..	..	0·697
	14. viii	8	..	..	..	3	4	1	..	..	..	..	..	..	..	..	..
	28. viii	89	..	..	..	13	71	5	..	..	..	..	..	..	..	..	0·674
	12. ix	11	..	..	2	5	4	..	..	..	..	..	..	..	..	..	0·646
	25. ix	2	..	..	..	1	1	..	..	..	..	..	..	..	..		..
	9. x	8	..	..	..	2	6	..	..	..	..	..	..	..	..		..
	23. x	2	..	..	..	..	2	..	..	..	..	..	..	..	..		..
	11. xii	2	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..
	28. i	4	..	..	..	1	1	2	..	..	..	..	..	..	..	..	..
VI ♀	6. i	112	..	..	..	..	1	27	66	17	1	..	..	..	..	..	0·745
	5. ii	92	..	..	..	..	..	20	57	13	2	..	..	..	..	..	0·785
	27. ii	85	..	..	..	..	2	19	23	14	17	10	..	..	..	..	0·812
	17. iii	120	..	..	..	..	..	16	37	15	20	24	6	2	..	..	0·832
	15. iv	137	..	..	..	..	..	1	5	3	9	23	36	43	15	2	1·017
	28. iv	115	..	..	..	..	..	..	..	..	..	8	20	40	37	10	1·062
	14. v	131	..	..	..	..	..	..	1	8	34	41	25	16	5	1	0·953
	2. vi	119	..	..	..	..	..	3	20	35	23	25	9	3	1	..	0·870
	18. vi	100	..	..	..	..	..	1	24	50	17	6	1	..	1	..	0·836
	3. vii	97	..	..	..	..	..	2	35	48	12	..	..	..	..	..	0·827
	17. vii	64	..	..	..	..	..	5	26	27	5	1	..	..	..	..	0·817
	31. vii	70	..	..	..	..	..	2	25	32	10	1	..	..	..	..	0·827
	14. viii	32	..	..	..	..	..	2	15	12	3	..	..	..	..	..	0·810
	28. viii	154	..	..	..	..	..	22	95	37	..	..	..	..	..	..	0·794
	12. ix	76	..	..	..	..	1	24	39	11	1	..	..	..	..	..	0·776
	25. ix	85	..	..	..	..	4	23	39	19	..	..	..	..	..	..	0·781
	9. x	94	..	..	..	..	..	27	54	11	2	..	..	..	..	..	0·784
	23. x	82	..	..	..	..	..	24	52	6	..	..	..	..	..	..	0·774
	17. xi	55	..	..	..	..	..	24	29	2	..	..	..	..	..	..	0·764
	26. xi	124	..	..	..	..	5	49	66	4	..	..	..	..	..	..	0·769
	11. xii	101	..	..	..	..	2	34	55	9	1	..	..	..	..	..	0·772
	28. i	92	..	..	..	..	..	17	40	20	13	1	1	..	..	..	0·794
V ♂	6. i	25	..	..	..	..	22	3	..	..	..	..					0·685
	5. ii	9	..	..	..	..	3	6	..	..	..	..	..	..	..	..	0·736
	27. ii	20	..	..	..	..	..	4	14	2	..	..	..	..	..	..	0·776
	17. iii	74	..	..	..	1	3	28	41	1	..	..	..	..	..	..	0·766
	3. iv	49	..	..	..	..	..	..	23	23	2	1	..	..	..	..	0·816
	28. iv	37	..	..	..	..	..	..	6	24	6	1	..	..	..	..	0·847

	14. v	31	..	..	..	1	3	12	10	2	3	..	..	..	..	..	0·758
	2. vi	29	..	..	..	..	12	14	2	1	..	..	..	..	..	..	0·714
	18. vi	19	..	..	..	1	9	6	2	1	..	..	..	..	..	..	0·706
	3. vii	36	..	..	..	1	24	8	3	..	..	..	..	..	..	..	0·695
	17. vii	32	..	..	..	1	12	19	..	..	..	..	..	..	..	..	0·714
	31. vii	64	..	..	..	..	28	35	1	..	..	..	..	..	..	..	0·711
	14. viii	23	..	..	..	..	22	1	..	..	..	..	..	..	..	..	0·684
	28. viii	102	..	..	..	12	77	12	1	..	..	..	..	..	..	..	0·686
	12. ix	63	..	..	..	9	46	8	..	..	..	..	..	..	..	..	0·676
	25. ix	36	..	..	..	2	25	9	..	..	..	..	..	..	..	..	0·688
	9. x	159	..	..	..	18	128	13	..	..	..	..	..	..	..	..	0·679
	23. x	20	..	..	..	2	15	3	..	..	..	..	..	..	..	..	0·687
	17. xi	3	..	..	..	..	3	..	..	..	..	..	..	..	..	..	..
	11. xii	4	..	..	..	..	3	1	..	..	..	..	..	..	..	..	..
V ♀	6. i	48	..	..	..	6	22	19	1	..	..	..	..	..	..	..	0·700
	5. ii	23	..	..	..	..	5	8	10	..	..	..	..	..	..	..	0·758
	27. ii	26	..	..	..	..	..	4	14	7	1	..	..	..	..	..	0·772
	17. iii	47	..	..	..	..	..	1	18	20	7	1	..	..	..	..	0·819
	3. iv	56	..	..	..	..	..	..	6	12	28	10	..	..	..	..	0·882
	28. iv	34	..	..	..	..	..	..	..	3	17	10	4	..	..	..	0·908
	14. v	36	..	..	..	..	2	6	18	4	5	1	..	..	..	..	0·767
	2. vi	33	..	..	..	..	15	18	..	..	..	..	..	..	..	..	0·712
	18. vi	42	..	..	..	..	6	20	10	6	..	..	..	..	..	..	0·750
	3. vii	38	..	..	..	..	4	28	6	..	..	..	..	..	..	..	0·735
	17. vii	54	..	..	..	..	14	29	11	..	..	..	..	..	..	..	0·729
	31. vii	31	..	..	..	..	1	25	4	1	..	..	..	..	..	..	0·731
	14. viii	18	..	..	..	..	7	10	1	..	..	..	..	..	..	..	0·714
	28. viii	93	..	..	..	7	49	36	1	..	..	..	..	..	..	..	0·699
	12. ix	52	..	..	..	11	31	10	..	..	..	..	..	..	..	..	0·677
	25. ix	38	..	..	..	2	23	12	1	..	..	..	..	..	..	..	0·699
	9. x	128	..	..	..	6	104	17	1	..	..	..	..	..	..	..	0·690
	23. x	11	..	..	..	1	8	2	..	..	..	..	..	..	..	..	0·693
	20. xi	2	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..
	11. xii	5	..	..	..	4	..	1	..	..	..	..	..	..	..	..	..
IV ♂	6. i	5	..	1	2	2	...	..	..	..	..	..	..	..	..	..	..
	5. ii	15	..	3	1	8	3	..	..	..	..	..	..	..	..	..	0·614
	27. ii	8	..	..	..	5	1	2	..	..	..	..	..	..	..	..	..
	17. iii	33	..	..	..	13	20	..	..	..	..	..	..	..	..	..	0·660
	3. iv	76	..	..	..	..	38	34	4	..	..	..	..	..	..	..	0·708
	28. iv	61	..	..	..	..	14	39	8	..	..	..	..	..	..	..	0·730
	14. v	16	..	..	3	5	8	..	..	..	..	..	..	..	..	..	0·655
	2. vi	30	..	..	5	25	..	..	..	..	..	..	..	..	..	..	0·622
	18. vi	10	..	..	1	5	4	..	..	..	..	..	..	..	..	..	0·638
	3. vii	11	..	..	..	9	2	..	..	..	..	..	..	..	..	..	0·615
	17. vii	17	..	..	4	13	..	..	..	..	..	..	..	..	..	..	0·625
	31. vii	67	..	..	4	55	8	..	..	..	..	..	..	..	..	..	0·639
	14. viii	34	..	..	15	19	..	..	..	..	..	..	..	..	..	..	0·606
	28. viii	81	..	..	30	50	1	..	..	..	..	..	..	..	..	..	0·608
	12. ix	135	..	1	61	71	2	..	..	..	..	..	..	..	..	..	0·604
	25. ix	66	..	..	15	48	3	..	..	..	..	..	..	..	..	..	0·610
	9. x	122	..	1	56	64	1	..	..	..	..	..	..	..	..	..	0·604
	23. x	2	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..
	11. xii	1	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..

TABLE X (*continued*)

Stage	Date	No.	0·442–0·495	0·495–0·548	0·548–0·602	0·602–0·655	0·655–0·708	0·708–0·761	0·761–0·813	0·813–0·867	Median size
IV ♀	6. i	4	..	..	..	4	..	..	..	..	..
	5. ii	21	..	..	1	13	7	..	..	..	..
	27. ii	18	..	..	..	2	14	2	..	..	0·630
	17. iii	47	..	..	..	6	25	16	..	..	0·668
	3. iv	69	..	..	..	3	8	49	9	..	0·693
	28. iv	73	..	..	..	..	6	41	24	2	0·735
	14. v	24	..	..	2	5	13	4	..	..	0·750
	2. vi	55	..	..	8	45	1	1	..	..	0·680
	18. vi	23	..	..	1	14	5	3	..	..	0·615
	3. vii	25	..	..	..	18	7	..	..	..	0·640
	17. vii	19	..	..	5	10	3	1	..	..	0·646
	31. vii	78	..	..	6	58	14	..	..	..	0·625
	14. viii	48	..	..	14	34	..	..	..	..	0·637
	28. viii	82	..	..	27	53	2	..	..	..	0·610
	12. ix	107	..	..	45	61	1	..	..	..	0·614
	25. ix	87	..	..	23	64	..	..	..	..	0·614
	9. x	132	..	..	51	81	..	..	..	..	0·614
	23. x	8	..	..	2	5	1	..	..	..	0·608
III	6. i	13	..	9	4	..	..	..	..	..	0·540
	5. ii	23	..	7	16	..	..	..	..	..	0·555
	27. ii	38	..	5	32	1	..	..	..	..	0·566
	17. iii	70	..	3	46	21	..	..	..	..	0·589
	3. iv	81	..	..	4	62	15	..	..	..	0·634
	28. iv	67	..	..	2	55	9	1	..	..	0·638
	14. v	26	..	4	16	6	..	..	..	..	0·587
	2. vi	51	..	38	13	..	..	..	..	..	0·534
	18. vi	15	1	6	8	..	..	..	..	..	0·550
	3. vii	23	2	17	4	..	..	..	..	..	0·522
	17. vii	4	..	1	3	..	..	..	..	..	..
	31. vii	82	..	24	58	..	..	..	..	..	0·558
	14. viii	28	..	26	2	..	..	..	..	..	0·528
	28. viii	61	5	53	3	..	..	..	..	..	0·523
	12. ix	54	2	51	1	..	..	..	..	..	0·518
	25. ix	42	..	36	6	..	..	..	..	..	0·532
	9. x	17	2	14	1	..	..	..	..	..	0·516

Stage	Date	No.	0·283–0·336	0·336–0·389	0·389–0·442	0·442–0·495	0·495–0·548	0·548–0·602	Median size
II	6. i	11	..	..	6	5	..	..	0·441
	5. ii	20	..	..	5	15	..	..	0·458
	27. ii	14	..	..	..	28	..	..	0·467
	17. iii	50	..	..	..	33	17	..	0·487
	3. iv	49	..	..	..	6	38	5	0·519
	28. iv	26	..	..	..	..	21	5	0·537
	14. v	21	..	..	..	12	9	..	0·493
	2. vi	26	..	..	16	10	..	..	0·438
	18. vi	24	..	..	1	20	3	..	0·467
	3. vii	30	..	..	16	14	..	..	0·439
	17. vii	10	..	..	3	7	..	..	0·452
	31. vii	41	..	..	2	39	..	..	0·463
	14. viii	35	..	..	27	8	..	..	0·432
	28. viii	17	..	..	15	2	..	..	0·431
	12. ix	41	..	..	34	7	..	..	0·435
	25. ix	16	..	..	6	10	..	..	0·448
	9. x	4	..	..	3	1	..	..	..
	23. x	2	..	..	1	1	..	..	..
I	6. i	19	..	18	1	..	..	..	0·366
	5. ii	46	..	36	10	..	..	..	0·376
	27. ii	46	..	38	8	..	..	..	0·380
	17. iii	90	..	34	56	..	..	..	0·394
	3. iv	78	..	16	58	4	..	..	0·406
	28. iv	21	..	..	19	1	..	..	0·426
	14. v	68	..	25	42	1	..	..	0·395
	2. vi	10	..	10	..	..	..	..	0·364
	18. vi	25	..	14	11	..	..	..	0·388
	3. vii	46	6	30	10	..	..	..	0·353
	17. vii	14	..	12	2	..	..	..	0·358
	31. vii	32	..	25	7	..	..	..	0·380
	14. viii	32	3	28	1	..	..	..	0·360
	28. viii	26	6	19	1	..	..	..	0·346
	12. ix	44	1	43	1	..	..	..	0·363
	25. ix	26	..	23	3	..	..	..	0·374
	9. x	5	..	5	..	..	..	..	..

TABLE XI. *PARACALANUS PARVUS*. SIZE IN MM.

Stage	Date	No.	0·442–0·495	0·495–0·548	0·548–0·602	0·602–0·655	0·655–0·708	0·708–0·761	0·761–0·813	0·813–0·867	0·867–9·020	Median size
VI ♂	6. i	3	..	..	1	2	..	..	..	..	..	..
	27. ii	1	..	..	..	..	..	1	..	..	..	..
	17. iii	6	..	..	..	..	1	4	1	..	..	..
	3. iv	3	..	..	..	..	..	2	1	..	..	..
	14. v	5	..	..	..	..	..	2	..	3	..	..
	17. vi	13	..	..	..	..	..	7	6	..	..	0·757
	3. vii	11	..	..	..	..	..	1	9	1	..	0·790
	17. vii	14	..	..	..	..	..	3	10	1	..	0·784
	14. viii	53	..	..	..	4	44	5	..	..	..	0·683
	28. viii	42	..	..	..	5	24	12	..	..	..	0·695
	12. ix	19	..	..	..	4	10	5	..	..	..	0·692
	25. ix	10	..	..	..	2	5	3	..	..	..	0·699
	9. x	16	..	..	..	4	6	6	..	..	..	0·705
	23. x	9	..	..	..	..	5	4	..	..	..	..
	17. xi	2	..	..	..	..	1	1	..	..	..	..
	20. xi	38	..	..	..	..	24	14	..	..	..	0·701
VI ♀	6. i	64	..	1	19	35	9	..	..	..	..	0·622
	5. ii	46	..	..	1	11	29	5	..	..	..	0·675
	27. ii	45	..	..	..	10	25	10	2	..	..	0·686
	17. iii	56	..	..	..	10	25	17	3	1	..	0·694
	3. iv	22	..	..	..	..	..	9	11	2	..	0·770
	15. iv	21	..	..	..	..	2	7	10	2	..	0·774
	28. iv	15	..	..	..	..	..	..	3	7	5	0·852
	14. v	25	..	..	..	..	..	7	10	8	..	0·777
	2. vi	7	..	..	..	2	4	1	..	..	..	..
	18. vi	60	..	..	..	4	33	20	2	1	..	0·699
	3. vii	70	..	..	..	7	17	41	5	..	..	0·719
	17. vii	67	..	..	..	..	13	45	..	9	..	0·739
	31. vii	36	..	..	..	2	12	19	3	..	..	0·720
	14. viii	234	..	..	44	143	40	7	..	..	..	0·628
	28. viii	227	..	..	12	152	56	7	..	..	..	0·643
	12. ix	220	..	..	14	134	57	15	..	..	..	0·640
	25. ix	153	..	..	10	72	51	18	2	..	..	0·651
	9. x	80	..	..	4	9	36	28	3	..	..	0·700
	23. x	81	..	..	..	7	49	25	..	..	..	0·695
	17. xi	60	..	..	..	2	44	14	..	..	..	0·692
	11. xii	80	..	..	3	15	49	13	..	..	..	0·680
V ♂	6. i	8	..	..	1	2	5	..	..	..	..	..
	5. ii	9	..	..	..	3	6	..	..	..	..	..
	27. ii	18	..	..	..	1	7	10	..	..	..	0·711
	17. iii	21	..	..	..	..	5	13	3	..	..	0·715
	3. iv	7	..	..	..	1	1	1	4	..	..	..
	14. v	2	..	..	..	..	..	..	2	..	..	..
	2. vi	8	..	..	1	1	5	1	..	..	..	..
	18. vi	13	..	..	..	..	6	6	1	..	..	0·710
	3. vii	18	..	..	..	..	3	15	..	..	..	0·729
	17. vii	8	..	..	..	1	..	6	1	..	..	..
	31. vii	16	..	..	..	2	7	7	..	..	..	0·704
	14. viii	5	..	..	12	93	51	..	..	..	..	0·647
	28. viii	..	..	..	1	26	39	..	..	..	..	0·660
	12. ix	114	..	..	2	63	46	3	..	..	..	0·650
	25. ix	37	..	..	..	15	20	2	..	..	..	0·663
	9. x	42	..	..	..	15	22	5	..	..	..	0·667
	23. x	13	..	..	..	2	10	1	..	..	..	0·678
	17. xi	16	..	..	..	5	10	1	..	..	..	0·664
	20. xi	18	..	..	1	9	8	..	..	..	..	0·651
V ♀	6. i	10	..	2	8	..	..	..	..	..	..	0·559
	5. ii	18	..	2	11	4	1	..	..	..	..	0·596
	27. ii	26	..	1	4	15	6	..	..	..	..	0·628
	17. iii	33	..	..	5	17	11	..	..	..	..	0·633
	3. iv	8	..	..	..	1	6	1	..	..	..	..
	28. iv	5	..	..	..	2	3	..	..	..	..	..
	14. v	7	..	..	..	3	3	1	..	..	..	..
	2. vi	28	..	4	22	2	..	..	..	..	..	0·576
	18. vi	16	..	..	8	7	1	..	..	..	..	0·602
	3. vii	12	..	..	1	10	1	..	..	..	..	0·629
	17. vii	4	..	..	..	2	2	..	..	..	..	..
	31. vii	9	..	..	1	8	..	..	..	..	..	..
	14. viii	216	3	109	96	8	..	..	..	..	..	0·548
	28. viii	135	..	30	94	10	1	..	..	..	..	0·568
	12. ix	186	..	43	128	14	1	..	..	..	..	0·565
	25. ix	56	..	13	32	11	..	..	..	..	..	0·569
	9. x	149	1	35	72	41	..	..	..	..	..	0·577
	23. x	33	..	7	17	14	..	..	..	..	..	0·591
	17. xi	13	..	3	10	..	..	..	..	..	..	0·561
	20. xi	20	1	7	2	..	..	..	..	..	..	0·553
IV ♂	6. i	6	..	6	..	..	..	..	..	..	..	..
	5. ii	8	..	2	6	..	..	..	..	..	..	..
	27. ii	18	..	2	16	..	..	..	..	..	..	0·575
	17. iii	12	..	3	7	2	..	..	..	..	..	0·588
	3. iv	6	..	..	..	5	1	..	..	..	..	..
	28. iv	3	..	..	..	3	..	..	..	..	..	..
	14. v	3	..	..	3	..	..	..	..	..	..	..
	2. vi	41	2	31	8	..	..	..	..	..	..	0·535
	18. vi	8	..	..	7	1	..	..	..	..	..	..
	3. vii	16	..	1	13	2	..	..	..	..	..	0·584

TABLE XI (*continued*)

Stage	Date	No.	0·336–0·389	0·389–0·442	0·442–0·495	0·495–0·548	0·548–0·602	0·602–0·655	Median size
IV ♂ (cont.)	17. vii	..	..	..	..	..	..	..	..
	31. vii	12	..	..	..	3	9	..	0·562
	14. viii	164	..	..	18	136	10	..	0·520
	28. viii	65	..	..	6	40	18	1	0·535
	12. ix	61	..	..	5	52	4	..	0·522
	25. ix	29	..	..	..	15	12	2	0·547
	9. x	25	..	..	1	17	7	..	0·533
	23. x	7	..	..	1	4	2	..	..
	17. xi	10	..	..	..	10	..	..	0·515
	20. xi	7	..	..	2	5	..	..	..
IV ♀	6. i	12	..	..	8	4	..	..	0·484
	5. ii	22	..	..	11	11	..	..	0·496
	27. ii	18	..	..	..	16	2	..	0·522
	17. iii	17	..	..	2	12	2	1	0·530
	3. iv	12	..	..	..	4	6	2	0·561
	28. iv	7	..	..	..	4	3	..	..
	14. v	11	..	..	..	10	1	..	0·529
	2. vi	71	..	..	57	14	..	..	0·475
	18. vi	22	..	..	1	20	1	..	0·517
	3. vii	15	..	..	..	15	..	..	0·519
	31. vii	15	..	..	5	10	..	..	0·505
	14. viii	203	..	19	177	7	..	..	0·460
	28. viii	97	..	4	84	9	..	..	0·477
	12. ix	83	..	8	65	10	..	..	0·469
	25. ix	34	..	1	16	16	1	..	0·495
	9. x	41	..	1	24	16	..	..	0·490
	23. x	24	..	2	10	10	2	..	0·459
	17. xi	17	..	..	16	1	..	..	0·473
	20. xi	13	..	4	9	..	..	..	0·457
III	6. i	27	..	23	4	..	..	..	0·417
	5. ii	25	7	16	2	..	..	..	0·413
	27. ii	33	..	16	17	..	..	..	0·444
	17. iii	12	..	3	9	..	..	..	0·451
	3. iv	12	..	2	5	5	..	..	0·487
	28. iv	9	..	..	8	1	..	..	..
	14. iv	17	..	7	8	2	..	..	0·455
	2. vi	91	2	73	16	..	..	..	0·421
	18. vi	18	..	9	9	..	..	..	0·443
	3. vii	21	..	15	6	..	..	..	0·431
	31. vii	13	..	11	2	..	..	..	0·423
	14. viii	82	16	66	..	..	..	..	0·403
	28. viii	35	2	31	2	..	..	..	0·412
	12. ix	76	15	58	3	..	..	..	0·402
	25. ix	32	1	25	6	..	..	..	0·423
	9. x	67	11	54	2	..	..	..	0·408
	23. x	50	2	45	3	..	..	..	0·418
	17. xi	21	5	16	..	..	..	..	0·398
	20. xi	22	14	8	..	..	..	..	0·385

Stage	Date	No.	0·177–0·230	0·230–0·283	0·283–0·336	0·336–0·389	0·389–0·442	0·442–0·495	Median size
II	6. i	24	..	..	13	11	..	..	0·334
	5. ii	33	..	..	6	27	..	..	0·353
	27. ii	9	..	..	1	8	..	..	..
	17. iii	18	..	..	4	13	1	..	0·380
	3. iv	18	..	..	1	13	4	..	0·377
	28. iv	8	..	..	..	6	2	..	..
	14. v	11	..	..	1	8	2	..	0·356
	2. vi	18	..	..	9	9	..	..	0·336
	18. vi	20	..	..	2	18	..	..	0·356
	3. vii	10	..	..	4	6	..	..	0·340
	17. vii	1	..	..	1	..	..	..	..
	31. vii	24	..	..	5	19	..	..	0·342
	14. viii	78	..	..	64	14	..	..	0·327
	28. viii	47	..	..	37	10	..	..	0·327
	12. ix	66	..	..	51	15	..	..	0·323
	25. ix	39	..	..	16	23	..	..	0·340
	9. x	48	..	..	31	17	..	..	0·331
	23. x	51	..	..	23	28	..	..	0·338
	17. xi	41	..	..	39	2	..	..	0·318
	20. x	35	..	..	1	34	..	..	0·304
I	6. i	1	..	1	..	..	..	..	..
	5. ii	27	..	17	10	..	..	..	0·275
	27. ii	30	..	22	7	1	..	..	0·276
	17. iii	43	..	27	16	..	..	..	0·279
	3. iv	20	..	8	12	..	..	..	0·287
	28. iv	15	..	2	13	..	..	..	0·297
	14. v	37	..	31	6	..	..	..	0·268
	2. vi	6	..	5	1	..	..	..	..
	18. vi	35	..	28	7	..	..	..	0·274
	3. vii	5	..	5	..	..	..	..	..
	17. vii	6	..	6	..	..	..	..	..
	31. vii	22	..	20	2	..	..	..	0·270
	14. viii	82	1	80	..	..	..	..	0·256
	28. viii	67	..	67	..	..	..	..	0·251
	12. ix	46	..	46	..	..	..	..	0·252
	25. ix	55	..	46	9	..	..	..	0·271
	9. x	54	..	54	..	..	..	..	0·255
	23. x	90	..	88	2	..	..	..	0·263
	17. xi	93	4	8	9	..	..	..	0·246
	20. xi	12	2	10	..	..	..	..	0·240

Table XII. *Centropages typicus*. Sizes in mm.

Stage	Date	No.	0·761–0·813	0·813–0·867	0·867–0·920	0·920–0·973	0·973–1·03	1·03–1·08	1·08–1·13	1·13–1·18	1·18–1·24	1·24–1·29	1·29–1·35	1·35–1·40	1·40–1·45	1·45–1·51	1·51–1·56	1·56–1·61	1·61–1·67	1·67–1·72
VI ♀	6. i	1	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	5. ii	3	1	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	3. iv	2	..	..	..	..	1	..	1	..	..	..	..	..	..	..	..	..	..	..
	14. v	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	2	1
	2. vi	2	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1	..	..
	18. vi	1	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..
	3. vii	11	..	..	..	..	..	..	..	..	..	1	..	5	3	2	..	..	..	..
	17. vii	1	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..
	31. vii	3	..	..	..	..	..	..	..	..	..	1	1	1	..	..	..	..	..	..
	14. viii	5	..	..	..	..	..	..	..	..	1	1	2	1	..	..	..	..	..	..
	28. viii	5	..	..	..	..	..	..	..	..	..	2	2	1	..	..	..	..	..	..
	4. ix	8	..	..	..	..	..	..	..	..	..	4	3	1	..	..	..	..	..	..
	25. ix	33	..	..	..	..	..	..	1	6	14	5	6	1	..	..	..	..	..	..
	23. x	1	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..
	17. xi	4	..	..	..	..	..	..	..	..	..	..	4	..	..	..	..	..	..	..
	20. xi	3	..	..	..	..	..	..	..	..	1	1	1	..	..	..	..	..	..	..
	11. xii	1	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..
	28. i	3		..	..	..	..	..	1	1	1	..	..	..	..	..	..	..	..	..

Table XIII. *Temora longicornis*. Size in mm.

Stage	Date	No.	0·548–0·602	0·602–0·655	0·655–0·708	0·708–0·761	0·761–0·813	0·813–0·867	0·867–0·920	0·920–0·973	0·973–1·03	1·03–1·08	1·08–1·13	1·13–1·18	1·18–1·24	1·24–1·29	1·29–1·35	1·35–1·40	1·40–1·45	Median size
VI ♂	6. i	3	..	..	..	..	..	..	..	2	1	..	..	..	..	..	..	..	..	..
	14. ii	3	..	..	..	..	..	1	..	1	1	..	..	..	..	..	..	..	..	..
	3. iv	4	..	..	..	..	..	..	1	2	..	1	..	..	..	..	..	..	..	..
	15. iv	8	..	..	..	..	..	..	1	3	3	1	..	..	..	..	..	..	..	..
	28. iv	2	..	..	..	..	..	..	..	..	..	..	2	..	..	..	..	..	..	..
	14. v	6	..	..	..	..	..	..	2	2	1	1	..	..	..	..	..	..	..	..
	2. vi	102	..	..	..	1	..	4	7	10	17	18	29	10	4	2	..	..	..	1·07
	18. vi	19	..	..	..	1	6	5	2	2	..	1	1	..	1	..	..	..	..	0·852
	3. vii	46	..	3	6	5	7	9	11	4	..	1	..	..	..	..	..	..	..	0·820
	17. vii	79	..	5	10	4	22	17	15	5	1	..	..	..	..	..	..	..	..	0·811
	31. vii	12	..	..	1	2	3	3	1	2	..	..	..	..	..	..	..	..	..	0·815
	14. viii	10	..	..	2	2	3	3	..	..	..	..	..	..	..	..	..	..	..	0·779
	28. viii	38	..	1	3	7	8	13	6	..	..	..	..	..	..	..	..	..	..	0·815
	12. ix	34	..	..	1	18	11	4	..	..	..	..	..	..	..	..	..	..	..	0·756
	25. ix	106	..	..	1	42	61	2	..	..	..	..	..	..	..	..	..	..	..	0·772
	9. x	2	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..
	23. x	2	..	..	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..
	17. xi	7	..	..	..	..	1	4	1	1	..	..	..	..	..	..	..	..	..	..
	26. xi	6	..	..	..	..	2	1	2	1	..	..	..	..	..	..	..	..	..	..
	11. xii	2	..	..	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..
VI ♀	5. ii	9	..	..	..	..	1	2	1	1	2	2	..	..	..	..	..	..	..	..
	14. ii	2	..	..	..	..	..	..	..	..	2	..	..	..	..	..	..	..	..	..
	27. ii	1	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..
	17. iii	1	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..
	3. iv	2	..	..	..	..	..	..	..	..	..	2	..	..	..	..	..	..	..	..
	15. iv	12	..	..	..	..	..	..	..	..	2	4	5	1	..	..	..	..	..	1·08
	28. iv	30	..	..	..	..	..	..	..	1	2	4	4	7	11	1	..	..	..	1·17
	14. v	17	..	..	..	..	..	..	..	..	4	3	2	3	1	2	1	1	..	1·11
	2. vi	75	..	..	..	..	2	3	5	4	5	7	11	8	14	8	4	3	1	1·14
	18. vi	14	..	..	..	..	..	1	1	4	5	2	..	..	1	..	..	..	..	0·983
	3. vii	48	..	..	5	6	10	7	8	7	3	2	..	..	..	..	..	..	..	0·851
	17. vii	68	..	..	10	8	8	16	11	9	4	2	..	..	..	..	..	..	..	0·839
	31. vii	9	..	..	..	1	1	1	2	2	2	..	..	..	..	..	..	..	..	..
	14. viii	7	..	..	..	..	..	4	1	1	1	..	..	..	..	..	..	..	..	..
	28. viii	47	..	..	..	5	13	12	12	4	..	1	..	..	..	..	..	..	..	0·840
	12. ix	18	..	..	1	5	6	3	3	..	..	..	..	..	..	..	..	..	..	0·797
	25. ix	120	..	..	5	14	36	48	15	2	..	..	..	..	..	..	..	..	..	0·819
	9. x	3	..	..	..	..	..	1	2	..	..	..	..	..	..	..	..	..	..	..
	23. x	4	..	..	..	..	1	1	..	..	..	2	..	..	..	..	..	..	..	..
	17. xi	11	..	..	..	..	..	4	3	2	..	1	1	..	..	..	..	..	..	0·894
	26. xi	16	..	..	..	..	1	2	3	5	3	2	..	..	..	..	..	..	..	0·956
	11. xii	5	..	..	..	..	..	1	4	..	..	..	..	..	..	..	..	..	..	..
V ♂	5. ii	3	..	..	..	..	1	2	..	..	..	..	..	..	..	..	..	..	..	..
	17. iii	1	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	3. iv	2	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..
	15. iv	2	..	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..
	28. iv	1	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..
	14. v	3	..	..	..	..	1	2	..	..	..	..	..	..	..	..	..	..	..	..
	2. vi	31	2	1	4	14	9	1	..	..	..	..	..	..	..	..	..	..	..	..
	18. vi	1	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0·735

Stage	Date	No.	0·177–0·230	0·230–0·283	0·283–0·336	0·336–0·389	0·389–0·442	0·442–0·449	0·495–0·548	0·548–0·602	0·602–0·655	0·655–0·708	0·708–0·761	0·761–0·813	0·813–0·816	0·816–0·920	0·920–0·973	Median size
V ♂	3. vii	20	..	..	..	..	..	..	..	1	1	6	10	2	..	..	..	0·729
	17. vii	8	..	..	..	..	..	..	..	..	..	5	2	1	..	..	..	..
	31. vii	3	..	..	..	..	..	..	..	..	1	1	1	..	..	..	..	..
	14. viii	17	..	..	..	..	..	..	..	..	6	6	5	..	..	..	..	0·680
	28. viii	80	..	..	..	..	..	..	..	..	12	52	16	..	..	..	..	0·686
	12. ix	9	..	..	..	..	..	..	..	1	6	1	1	..	..	..	..	..
	25. ix	30	..	..	..	..	..	..	..	1	6	17	5	1	..	..	..	0·673
	9. x	1	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..
V ♀	5. ii	5	..	..	..	..	..	..	..	..	..	..	3	1	..	1	..	..
	3. iv	6	..	..	..	..	..	..	..	..	..	..	..	1	3	2	..	..
	15. iv	3	..	..	..	..	..	..	..	..	..	..	..	..	2	1	..	..
	28. iv	7	..	..	..	..	..	..	..	..	..	..	1	..	1	2	3	..
	14. v	8	..	..	..	..	..	..	..	..	..	1	1	3	2	..	1	..
	2. vi	21	..	..	..	..	..	..	..	1	..	2	5	12	1	..	..	0·770
	18. vi	3	..	..	..	..	..	..	..	..	..	..	1	2	..	..	..	..
	3. vii	35	..	..	..	..	..	..	..	..	2	3	17	13	..	..	..	0·750
	17. vii	14	..	..	..	..	..	..	..	..	..	3	8	2	1	..	..	0·725
	31. vii	1	..	..	..	....	..	..	..	..	..	..	1	..	..	..	..	..
	14. viii	40	..	..	..	..	..	..	..	..	1	23	14	2	..	..	..	0·699
	28. viii	64	..	..	..	..	..	..	..	..	9	27	28	..	..	..	..	0·700
	12. ix	12	..	..	..	..	..	..	..	..	8	2	2	..	..	..	..	0·650
	25. ix	16	..	..	..	..	..	..	..	..	4	16	6	..	..	..	..	0·688
	9. x	1	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..
	23. x	1	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..
	26. x	1	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..
IV ♂	5. ii	1	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..
	17. iii	1	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..
	3. iv	1	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..
	15. iv	1	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..
	14. v	2	..	..	..	..	..	..	..	..	1	..	..	1	..	..	..	..
	2. vi	9	..	..	..	..	..	..	1	7	1	..	..	..	..	..	..	..
	3. vii	1	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..
	31. vii	2	..	..	..	..	..	..	..	..	2	..	..	..	..	..	..	..
	14. viii	19	..	..	..	..	..	1	10	8	..	..	..	..	..	..	..	0·545
	28. viii	19	..	..	..	..	..	..	5	14	..	..	..	..	..	..	..	0·557
	12. ix	3	..	..	..	..	..	..	..	3	..	..	..	..	..	..	..	..
	25. ix	11	..	..	..	..	..	..	3	7	1	..	..	..	..	..	..	0·568
IV ♀	14. ii	1	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..
	17. iii	2	..	..	..	..	..	..	..	..	1	1	..	..	..	..	..	..
	3. iv	7	..	..	..	..	..	..	..	..	1	4	2	..	..	..	..	..
	15. iv	2	..	..	..	..	..	..	..	..	2	..	..	..	..	..	..	..
	28. iv	4	..	..	..	..	..	..	..	..	..	2	2	..	..	..	..	..
	14. v	9	..	..	..	..	..	..	..	3	3	3	..	..	..	..	..	..
	2. vi	34	..	..	..	..	..	2	5	14	10	3	..	..	..	..	..	0·590
	18. vi	15	..	..	..	..	..	..	..	3	8	4	..	..	..	..	..	0·622
	3. vi	36	..	..	..	..	..	..	..	17	17	2	..	..	..	..	..	0·604
	17. vii	1	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..
	14. viii	79	..	..	..	..	..	..	27	50	2	..	..	..	..	..	..	0·562
	28. viii	198	..	..	..	..	..	..	63	122	13	..	..	..	..	..	..	0·560
	12. ix	24	..	..	..	..	..	..	16	6	2	..	..	..	..	..	..	0·542
	25. ix	27	..	..	..	..	..	..	7	15	5	..	..	..	..	..	..	0·525
	9. x	1	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..

Table XIII (*continued*)

Stage	Date	No.	0·177–0·230	0·230–0·283	0·283–0·336	0·336–0·389	0·389–0·442	0·442–0·495	0·495–0·548	0·548–0·602	0·602–0·655	0·655–0·708	0·708–0·761	0·761–0·813	0·813–0·867	0·867–0·920	0·920–0·973	Median size
III	5. ii	1	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..
	27. ii	1	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..
	3. iv	..	..	..	..	..	..	..	1	2	..	..	..	..	..	..	..	..
	28. iv	10	..	..	..	..	..	..	5	4	1	..	..	..	..	..	..	0·557
	14. v	6	..	..	..	..	..	1	3	2	..	..	..	..	..	..	..	..
	2. vi	40	..	..	..	..	4	33	3	..	..	..	..	..	..	..	..	0·466
	18. vi	15	..	..	..	..	..	7	8	..	..	..	..	..	..	..	..	0·497
	3. vii	21	..	..	..	..	1	13	6	1	..	..	..	..	..	..	..	0·485
	17. vii	1	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..
	31. vii	2	..	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..
	14. viii	97	..	..	..	..	21	74	2	..	..	..	..	..	..	..	..	0·455
	28. viii	78	..	..	..	..	22	55	1	..	..	..	..	..	..	..	..	0·452
	12. ix	17	..	..	..	..	4	12	1	..	..	..	..	..	..	..	..	0·459
	25. ix	8	..	..	..	..	..	4	4	..	..	..	..	..	..	..	..	..
	9. x	2	..	..	..	..	..	..	2	..	..	..	..	..	..	..	..	..
	23. x	1	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..
II	27. ii	2	..	..	..	2	..	..	..	..	..	..	..	..	..	..	..	..
	17. iii	10	..	..	..	..	10	..	..	..	..	..	..	..	..	..	..	0·412
	3. iv	6	..	..	..	..	5	1	..	..	..	..	..	..	..	..	..	..
	28. iv	9	..	..	..	..	3	6	..	..	..	..	..	..	..	..	..	..
	14. v	21	..	..	..	..	20	1	..	..	..	..	..	..	..	..	..	0·417
	2. vi	25	..	..	..	18	7	..	..	..	..	..	..	..	..	..	..	0·382
	18. vi	25	..	..	..	2	23	..	..	..	..	..	..	..	..	..	..	0·418
	3. vii	15	..	..	..	6	9	..	..	..	..	..	..	..	..	..	..	0·395
	31. vii	8	..	..	..	3	5	..	..	..	..	..	..	..	..	..	..	..
	14. viii	38	..	..	1	37	..	..	..	..	..	..	..	..	..	..	..	0·366
	28. viii	47	..	..	..	33	14	..	..	..	..	..	..	..	..	..	..	0·374
	12. ix	7	..	..	..	5	2	..	..	..	..	..	..	..	..	..	..	..
	25. ix	11	..	..	..	5	6	..	..	..	..	..	..	..	..	..	..	0·396
	9. x	1	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..
I	5. ii	2	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..
	27. ii	3	..	1	2	..	..	..	..	..	..	..	..	..	..	..	..	0·325
	17. iii	42	..	..	36	6	..	..	..	..	..	..	..	..	..	..	..	..
	3. iv	6	..	..	4	2	..	..	..	..	..	..	..	..	..	..	..	0·344
	28. iv	1	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..
	14. v	37	..	..	9	28	..	..	..	..	..	..	..	..	..	..	..	0·302
	2. vi	21	..	..	21	..	..	..	..	..	..	..	..	..	..	..	..	0·338
	18. vi	23	..	..	10	13	..	..	..	..	..	..	..	..	..	..	..	..
	3. vii	5	..	..	4	1	..	..	..	..	..	..	..	..	..	..	..	..
	17. vii	1	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..
	31. vii	14	..	..	14	..	..	..	..	..	..	..	..	..	..	..	..	..
	14. viii	52	..	10	42	..	..	..	..	..	..	..	..	..	..	..	..	0·309
	28. viii	23	..	3	20	..	..	..	..	..	..	..	..	..	..	..	..	0·294
	12. ix	8	..	8	..	..	..	..	..	..	..	..	..	..	..	..	..	0·294
	25. ix	14	..	..	13	1	..	..	..	..	..	..	..	..	..	..	..	..

Table XIV. *Acartia clausi*. Size in mm.

Stage	Date	No.	0·602–0·655	0·655–0·708	0·708–0·761	0·761–0·814	0·814–0·867	0·867–0·920	0·920–0·973	0·973–1·03	1·03–1·08	1·08–1·13	1·13–1·18	Median size
VI ♂	14. ii	2	..	..	..	1	1	..	..	..	..	..	..	..
	3. iv	2	..	..	..	..	2	..	..	..	..	..	..	..
	15. iv	37	..	..	..	..	..	..	23	14	..	..	..	0·966
	28. iv	16	..	..	..	..	..	..	13	3	..	..	..	0·965
	14. v	36	..	..	..	..	..	6	28	2	..	..	..	0·943
	2. vi	88	..	..	..	..	7	74	7	..	..	..	..	0·894
	18. vi	35	..	..	..	..	18	16	1	..	..	..	..	0·866
	3. vii	96	..	..	..	1	56	37	2	..	..	..	..	0·860
	17. vii	122	..	..	1	6	81	31	3	..	..	..	..	0·852
	31. vii	87	..	..	..	1	67	19	..	..	..	..	..	0·847
	14. viii	65	..	..	4	44	16	1	..	..	..	..	..	0·798
	28. viii	46	..	..	1	30	15	..	..	..	..	..	..	0·807
	12. ix	30	..	..	1	17	12	..	..	..	..	..	..	0·810
	25. ix	29	..	..	..	25	4	..	..	..	..	..	..	0·802
	9. x	5	..	..	..	2	3	..	..	..	..	..	..	..
	17. xi	3	..	..	..	..	3	..	..	..	..	..	..	..
	26. xi	17	..	..	..	2	15	..	..	..	..	..	..	0·836
	11. xii	2	..	..	..	..	2	..	..	..	..	..	..	..
	7. i	6	..	..	..	1	3	2	..	..	..	..	..	..
	28. i	1	..	..	..	..	1	..	..	..	..	..	..	..
VI ♀	6. i	9	..	..	..	1	2	5	1	..	..	..	..	..
	5. ii	3	..	..	..	2	..	1	..	..	..	..	..	..
	14. ii	12	..	..	..	2	7	2	1	..	..	..	..	0·838
	27. ii	3	..	..	..	..	2	1	..	..	..	..	..	..
	17. iii	41	..	..	..	7	21	18	..	..	..	..	..	0·851
	3. iv	6	..	..	..	2	1	1	..	..	..	1	1	..
	15. iv	17	..	..	..	..	..	..	..	..	4	11	2	1·10
	28. iv	63	..	..	..	..	..	..	..	..	2	40	21	1·12
	14. v	80	..	..	..	..	..	3	3	3	29	32	10	1·08
	2. vi	92	..	..	..	..	..	2	22	45	19	3	1	0·992
	18. vi	31	..	..	..	..	..	5	16	9	1	..	..	0·960
	3. vii	76	..	..	..	..	..	14	49	13	..	..	..	0·944
	17. vii	138	..	..	..	..	1	34	84	17	1	1	..	0·936
	31. vii	54	..	..	..	..	..	13	35	6	..	..	..	0·936
	14. viii	69	..	..	..	17	32	16	4	..	..	..	..	0·836
	28. viii	62	..	..	..	13	29	17	3	..	..	..	..	0·845
	12. ix	59	..	..	..	9	35	15	..	..	..	..	..	0·845
	25. ix	105	..	..	1	30	61	13	..	..	..	..	..	0·834
	9. x	46	..	..	2	11	23	10	..	..	..	..	..	0·834
	23. x	8	..	..	1	2	3	2	..	..	..	..	..	..
	17. xi	9	..	..	1	2	4	2	..	..	..	..	..	..
	26. xi	21	..	1	4	4	9	3	..	..	..	..	..	0·824
	11. xii	6	..	..	..	3	3	..	..	..	..	..	..	..
	7. i	12	..	..	..	1	3	6	2	..	..	..	..	0·876
	28. i	15	..	..	1	1	6	4	3	..	..	..	..	0·865
V ♂	17. ii	1	..	..	1	..	..	..	..	..	..	..	..	..
	3. iv	4	..	..	4	..	..	..	..	..	..	..	..	..
	15. iv	15	..	..	..	..	12	3	..	..	..	..	..	0·851
	28. iv	2	..	..	..	..	1	1	..	..	..	..	..	..
	14. v	50	..	..	1	23	26	..	..	..	..	..	..	0·815
	2. vi	51	..	..	11	40	..	..	..	..	..	..	..	0·773
	18. vi	24	..	..	3	19	2	..	..	..	..	..	..	0·787
	3. vii	20	..	1	14	5	..	..	..	..	..	..	..	0·750
	17. vii	1	..	..	1	..	..	..	..	..	..	..	..	..
	31. vii	12	..	..	8	4	..	..	..	..	..	..	..	0·755
	14. viii	25	2	17	6	..	..	..	..	..	..	..	..	0·700
	28. viii	12	..	3	9	..	..	..	..	..	..	..	..	0·714
	12. ix	9	..	6	3	..	..	..	..	..	..	..	..	..
	25. ix	10	1	4	5	..	..	..	..	..	..	..	..	..
	9. x	1	..	..	1	..	..	..	..	..	..	..	..	0·707
V ♀	17. xi	3	..	..	3	..	..	..	..	..	..	..	..	..
	5. ii	2	..	..	..	..	..	2	..	..	..	..	..	..
	14. ii	2	..	..	..	..	..	1	1	..	..	..	..	..
	17. iii	1	..	..	..	..	..	1	..	..	..	..	..	..
	3. iv	1	..	..	..	..	..	..	1	..	..	..	..	..
	15. iv	8	..	..	..	..	..	3	4	1	..	..	..	..
	28. iv	6	..	..	..	..	..	4	2	..	..	..	..	..
	14. v	35	..	..	..	2	18	15	..	..	..	..	..	0·859
	2. vi	44	..	..	3	31	10	..	..	..	..	..	..	0·792
	18. vi	25	..	..	..	5	13	7	..	..	..	..	..	0·845
	3. vii	15	..	..	5	8	2	..	..	..	..	..	..	0·776
	17. vii	7	..	..	2	5	..	..	..	..	..	..	..	..
	31. vii	16	..	..	3	13	..	..	..	..	..	..	..	0·784
	14. viii	42	..	27	15	..	..	..	..	..	..	..	..	0·700
	28. viii	20	..	6	14	..	..	..	..	..	..	..	..	0·715
	12. ix	29	..	20	9	..	..	..	..	..	..	..	..	0·693
	25. ix	26	..	11	14	1	..	..	..	..	..	..	..	0·714
	9. x	10	1	9	..	..	..	..	..	..	..	..	..	0·672

Table XIV (*continued*)

Stage	Date	No.	0·283–0·336	0·336–0·389	0·389–0·442	0·442–0·495	0·495–0·548	0·548–0·602	0·602–0·655	0·655–0·708	0·708–0·761	0·761–0·813	Median size
IV ♂	17. iii	1	..	..	..	..	..	..	1	..	..	..	..
	3. iv	4	..	..	..	..	..	..	..	..	4	..	..
	15. iv	15	..	..	..	..	..	..	..	2	13	..	0·729
	28. iv	3	..	..	..	..	..	..	..	..	3	..	..
	14. v	53	..	..	..	..	..	..	9	33	11	..	0·689
	2. vi	26	..	..	..	..	..	..	22	4	..	..	0·640
	18. vi	16	..	..	..	..	..	..	14	2	..	..	0·664
	3. vii	25	..	..	..	..	..	1	21	3	..	..	0·638
	17. vii	2	..	..	..	..	..	1	1	..	..	..	..
	31. vii	17	..	..	..	..	..	..	15	2	..	..	0·645
	14. viii	26	..	..	..	..	..	13	13	..	..	..	0·602
	28. viii	10	..	..	..	..	..	4	6	..	..	..	0·605
	12. ix	22	..	..	..	..	..	13	9	..	..	..	0·596
	25. ix	4	..	..	..	..	..	2	2	..	..	..	..
	9. x	4	..	..	..	..	..	1	3	..	..	..	..
	17. xi	2	..	..	..	..	..	..	2	..	..	..	..
IV ♀	5. ii	2	..	..	..	..	..	1	1	..	..	..	..
	17. iii	1	..	..	..	..	..	..	1	..	..	..	..
	3. iv	1	..	..	..	..	..	..	..	..	..	1	..
	15. iv	14	..	..	..	..	..	..	..	..	8	6	0·758
	28. iv	7	..	..	..	..	..	..	..	..	4	3	..
	14. v	65	..	..	..	..	..	1	2	29	33	..	0·710
	2. vi	34	..	..	..	..	..	1	19	14	..	..	0·650
	18. vi	15	..	..	..	..	..	..	..	13	2	..	0·685
	3. vii	17	..	..	..	..	..	1	10	6	..	..	0·648
	17. vii	2	..	..	..	..	..	..	1	1	..	..	0·650
	31. vii	22	..	..	..	..	..	..	13	9	..	..	0·595
	14. viii	23	..	..	..	..	..	16	6	1	..	..	0·595
	28. viii	45	..	..	..	..	..	30	15	..	..	..	0·590
	12. ix	37	..	..	..	..	2	21	14	..	..	..	..
	25. ix	9	..	..	..	..	..	6	3	..	..	..	..
	9. x	3	..	..	..	..	..	2	1	..	..	..	..
	17. xi	6	..	..	..	..	..	2	4	..	..	..	..
III	5. ii	1	..	..	..	..	..	1	..	..	..	..	..
	17. iii	1	..	..	..	..	..	1	..	..	..	..	..
	3. iv	4	..	..	..	..	2	2	..	..	..	..	..
	15. iv	5	..	..	..	..	..	..	4	1	..	..	..
	28. iv	8	..	..	..	..	..	..	7	1	..	..	..
	14. v	31	..	..	..	..	..	17	14	..	..	..	0·600
	2. vi	56	..	..	..	1	43	12	..	..	..	..	0·536
	18. vi	34	..	..	..	..	7	26	1	..	..	..	0·569
III	3. vii	28	..	..	..	1	22	5	..	..	..	..	..
	17. vii	6	..	..	..	..	5	1	..	..	..	..	..
	31. vii	36	..	..	..	..	25	11	..	..	..	..	0·529
	14. viii	44	..	..	..	15	28	1	..	..	..	..	0·542
	28. viii	18	..	..	..	4	13	1	..	..	..	..	0·502
	12. ix	9	..	..	..	6	3	..	..	..	..	..	0·505
	25. ix	3	..	..	..	1	2	..	..	..	..	..	..
	9. x	2	..	..	..	..	2	..	..	..	..	..	..
	17. xi	3	..	..	..	..	3	..	..	..	..	..	..
	11. xii	1	..	..	..	..	1	..	..	..	..	..	..
II	17. iii	1	..	..	1	..	..	..	..	..	..	..	..
	3. iv	6	..	..	..	2	2	2	..	..	..	..	..
	28. iv	13	..	..	..	3	10	..	..	..	..	..	0·516
	14. v	38	..	..	..	16	22	..	..	..	..	..	0·498
	2. vi	48	..	..	34	14	..	..	..	..	..	..	0·434
	18. vi	36	..	..	..	35	1	..	..	..	..	..	0·455
	3. vii	20	..	..	4	16	..	..	..	..	..	..	0·453
	17. vii	7	..	..	6	1	..	..	..	..	..	..	0·443
	31. vii	49	..	..	24	25	..	..	..	..	..	..	..
	14. viii	8	..	1	7	..	..	..	..	..	..	..	..
	28. viii	3	..	..	3	..	..	..	..	..	..	..	..
	12. ix	2	..	..	2	..	..	..	..	..	..	..	..
	25. ix	1	..	..	1	..	..	..	..	..	..	..	..
	9. x	2	..	1	1	..	..	..	..	..	..	..	..
	23. x	3	..	..	3	..	..	..	..	..	..	..	..
	17. xi	8	..	..	7	1	..	..	..	..	..	..	..
	11. xii	4	..	..	3	1	..	..	..	..	..	..	..
I	17. iii	1	..	1	..	..	..	..	..	..	..	..	..
	3. iv	10	..	..	10	..	..	..	..	..	..	..	0·415
	28. iv	17	..	1	15	1	..	..	..	..	..	..	0·427
	14. v	35	..	15	20	..	..	..	..	..	..	..	0·392
	2. vi	23	2	21	..	..	..	..	..	..	..	..	0·356
	18. vi	34	..	29	5	..	..	..	..	..	..	..	0·369
	3. vii	19	1	17	1	..	..	..	..	..	..	..	0·356
	17. vii	7	1	6	..	..	..	..	..	..	..	..	..
	31. vii	82	5	77	..	..	..	..	..	..	..	..	0·331
	14. viii	6	6	..	..	..	..	..	..	..	..	..	..
	28. viii	10	7	3	..	..	..	..	..	..	..	..	0·338
	12. ix	1	1	..	..	..	..	..	..	..	..	..	..
	25. ix	5	..	5	..	..	..	..	..	..	..	..	..
	9. x	3	2	1	..	..	..	..	..	..	..	..	..
	23. x	4	3	1	..	..	..	..	..	..	..	..	..
	17. xi	7	1	5	1	..	..	..	..	..	..	..	..
	11. xii	2	..	2	..	..	..	..	..	..	..	..	..

TABLE XV. *OITHONA SIMILIS*. SIZE IN MM.

Stage	Date	No.	0·301–0·336	0·336–0·372	0·372–0·407	0·407–0·442	0·442–0·477	0·477–0·513	0·513–0·548	0·548–0·584	Median size
VI ♂	6. i	12	..	..	4	6	2	..	..	..	0·428
	5. ii	9	..	..	..	3	5	1	..	..	..
	27. ii	7	..	..	..	1	6	..	..	..	..
	17. iii	6	..	..	..	2	1	3	..	..	..
	3. iv	14	..	..	..	..	1	12	1	..	0·493
	28. iv	9	..	..	..	..	..	9	..	..	..
	14. v	16	..	..	..	..	9	4	2	1	0·475
	2. vi	12	..	..	..	1	6	5	..	..	0·474
	18. vi	23	..	..	..	3	17	3	..	..	0·461
	3. vii	16	..	..	..	2	14	..	..	..	0·453
	17. vii	33	..	..	2	21	10	..	..	..	0·435
	31. vii	41	..	..	3	20	18	..	..	..	0·440
	14. viii	31	..	..	2	26	3	..	..	..	0·427
	28. viii	19	..	..	1	17	1	..	..	..	0·430
	12. ix	7	..	..	..	6	1	..	..	..	..
	25. ix	11	..	..	1	9	1	..	..	..	0·433
	9. x	6	..	..	1	5	..	..	..	..	..
	23. x	2	..	..	2	..	..	..	..	..	..
	17. xi	9	..	..	3	6	..	..	..	..	..
	11. xii	3	..	..	1	2	..	..	..	..	..
VI ♀	6. i	68	..	..	6	33	29	..	..	..	0·438
	5. ii	31	..	..	4	13	12	2	..	..	0·438
	27. ii	41	..	..	..	6	22	13	..	..	0·467
	17. iii	102	..	..	..	11	47	36	8	..	0·473
	3. iv	64	..	..	..	2	13	15	17	17	0·517
	28. iv	47	..	..	..	..	3	13	25	6	0·533
	14. v	43	..	..	..	..	1	15	25	3	0·523
	2. vi	54	..	..	..	..	17	24	10	3	0·491
	18. vi	66	..	..	..	1	40	25	..	..	0·474
	3. vii	63	..	..	..	1	32	29	1	..	0·477
	17. vii	186	..	..	..	49	121	15	1	..	0·453
	31. vii	173	..	..	..	13	129	25	5	1	0·465
	14. viii	179	..	..	4	100	72	3	..	..	0·439
	28. viii	109	..	..	2	37	51	17	2	..	0·448
	12. ix	148	..	..	4	88	53	3	..	..	0·438
	25. ix	116	..	..	1	69	45	1	..	..	0·438
	9. x	61	..	..	4	45	12	..	..	..	0·430
	23. x	31	..	..	2	23	5	..	..	..	0·430
	17. xi	38	..	..	2	23	13	..	..	..	0·435
	11. xii	28	..	..	1	12	15	..	..	..	0·444
V ♂	6. i	29	..	..	9	12	8	..	..	..	0·417
	5. ii	22	..	1	9	5	7	..	..	..	0·428
	27. ii	20	..	..	..	1	12	7	..	..	0·460
	17. iii	38	..	..	2	11	22	3	..	..	0·457
	3. iv	64	..	..	..	..	7	47	10	..	0·498
	28. iv	20	..	..	..	..	3	14	3	..	0·494
	14. v	46	..	..	..	13	18	15	..	..	0·460
	2. vi	15	..	..	..	33	39	3	..	..	0·447
	18. vi	69	..	..	2	37	29	1	..	..	0·440
	3. vii	55	..	..	1	24	30	..	..	..	0·445
	17. vii	104	..	..	40	57	7	..	..	..	0·414
	31. vii	102	..	..	6	54	42	..	..	..	0·437
	14. viii	104	..	1	46	52	2	..	..	..	0·409
	28. viii	82	..	1	30	42	8	..	..	..	0·419
	12. ix	108	..	..	33	71	4	..	..	..	0·419
	25. ix	70	..	..	16	44	10	..	..	..	0·426
	9. x	58	..	1	29	27	1	..	..	..	0·406
	23. x	47	..	4	25	18	..	..	..	..	0·402
	17. xi	18	..	..	6	12	..	..	..	..	0·418
	11. xii	28	..	..	3	17	8	..	..	..	0·434
IV	6. i	8	..	4	4	..	..	..	..	..	..
	5. ii	28	7	9	10	2	..	..	..	..	0·354
	27. ii	10	..	2	6	1	1	..	..	..	0·389
	17. iii	25	..	7	5	13	..	..	..	..	0·401
	3. iv	56	..	..	5	32	18	1	..	..	0·417
	28. iv	16	..	..	1	9	6	..	..	..	0·438
	14. v	36	..	5	12	19	..	..	..	..	0·423
	2. vi	44	..	3	29	12	..	..	..	..	0·397
	18. vi	60	..	9	46	5	..	..	..	..	0·388
	3. vii	26	..	5	20	1	..	..	..	..	0·388
	17. vii	103	..	80	23	..	..	..	..	..	0·360
	31. vii	103	..	20	82	1	..	..	..	..	0·384
	14. viii	79	3	63	13	..	..	..	..	..	0·358

TABLE XV (*continued*)

Stage	Date	No.	0·301–0·336	0·336–0·372	0·372–0·407	0·407–0·442	0·442–0·477	0·477–0·513	0·513–0·548	0·458–0·584	Median size
IV	28. viii	35	..	20	15	..	..	..	..	..	0·369
	12. ix	108	2	70	36	..	..	..	..	..	0·365
	25. ix	21	..	5	16	..	..	..	..	..	0·380
	9. x	36	2	29	5	..	..	..	..	..	0·353
	23. x	29	1	22	6	..	..	..	..	..	0·358
	17. xi	14	..	8	6	..	..	..	..	..	0·379
	11. xii	28	..	11	14	3	..	..	..	..	0·378

	Date	No.	0·159–0·195	0·195–0·230	0·230–0·265	0·265–0·301	0·301–0·336	0·336–0·372	0·372–0·407	0·407–0·442	Median size
III	6. i	13	..	..	..	..	7	6	..	..	0·334
	5. ii	26	..	..	..	3	19	4	..	..	0·321
	27. ii	19	..	..	..	..	5	13	1	..	0·343
	17. iii	23	..	..	..	..	1	11	11	..	0·371
	3. iv	43	..	..	..	..	..	7	36	..	0·382
	28. iv	24	..	..	..	..	..	1	23	..	0·384
	14. v	25	..	..	..	..	12	10	3	..	0·339
	2. vi	42	..	..	..	1	11	30	..	..	0·346
	18. vi	36	..	..	..	..	11	25	..	..	0·344
	3. vii	42	..	..	..	..	8	34	..	..	0·346
	17. vii	87	..	..	..	6	78	3	..	..	0·314
	31. vii	37	..	..	..	..	15	22	..	..	0·339
	14. viii	61	..	..	..	5	56	..	..	..	0·313
	28. viii	44	..	..	..	..	37	7	..	..	0·328
	12. ix	96	..	..	..	7	80	9	..	..	0·321
	25. ix	33	..	..	..	..	16	17	..	..	0·337
	9. x	29	..	..	..	1	28	..	..	..	0·318
	23. x	27	..	..	..	..	22	5	..	..	0·326
	17. xi	13	..	..	..	..	10	3	..	..	0·328
	11. xii	24	..	..	..	..	5	19	..	..	0·346
II	6. i	7	..	..	..	7	..	..	..	..	..
	5. ii	15	..	..	7	7	1	..	..	..	0·274
	27. ii	12	..	..	1	11	..	..	..	..	0·277
	17. iii	38	..	..	..	18	20	..	..	..	0·302
	3. iv	45	..	..	..	13	31	1	..	..	0·307
	28. iv	20	..	..	..	7	13	..	..	..	0·305
	14. v	35	..	..	9	15	11	..	..	..	0·291
	2. vi	66	..	..	..	65	1	..	..	..	0·282
	18. vi	67	..	..	14	53	..	..	..	..	0·274
	3. vii	36	..	..	1	34	1	..	..	..	0·284
	17. vii	30	..	1	26	3	..	..	..	..	0·255
	31. vii	51	..	..	10	41	..	..	..	..	0·274
	14. viii	42	..	..	35	7	..	..	..	..	0·257
	28. viii	59	..	..	32	27	..	..	..	..	0·264
	12. ix	121	..	..	78	43	..	..	..	..	0·261
	25. ix	37	..	..	6	31	..	..	..	..	0·275
	9. x	30	..	..	27	3	..	..	..	..	0·254
	23. x	27	..	..	2	25	..	..	..	..	0·276
	17. xi	9	..	..	3	6	..	..	..	..	..
	11. xii	19	..	..	4	15	..	..	..	..	0·280
I	6. i	4	..	1	3	..	..	..	..	..	..
	5. ii	9	..	4	4	1	..	..	..	..	..
	27. ii	24	..	16	8	..	..	..	..	..	0·225
	17. iii	39	..	18	21	..	..	..	..	..	0·231
	3. iv	35	..	10	25	..	..	..	..	..	0·236
	28. iv	15	..	5	10	..	..	..	..	..	0·235
	14. v	27	1	11	15	..	..	..	..	..	0·232
	2. vi	78	..	55	23	..	..	..	..	..	0·225
	18. vi	55	..	49	6	..	..	..	..	..	0·219
	3. vii	43	..	35	8	..	..	..	..	..	0·222
	17. vii	39	7	31	1	..	..	..	..	..	0·204
	31. vii	70	..	69	1	..	..	..	..	..	0·215
	14. viii	71	14	57	..	..	..	..	..	..	0·202
	28. viii	59	2	57	..	..	..	..	..	..	0·204
	12. ix	90	..	90	..	..	..	..	..	..	0·208
	25. ix	57	..	46	11	..	..	..	..	..	0·222
	9. x	33	1	32	..	..	..	..	..	..	0·204
	23. x	28	..	28	..	..	..	..	..	..	0·219
	17. xi	19	..	19	..	..	..	..	..	..	0·213
	11. xii	..	..	8	..	..	..	..	..	..	..

TABLE XVI. *OITHONA NANA*. SIZE IN MM.

Stage	Date	No.	0·124–0·159	0·159–0·195	0·195–0·230	0·230–0·265	0·265–0·301	0·301–0·336	0·336–0·372	0·372–0·407	Median size
VI ♂	12. ix	8	..	..	..	..	1	7	..	..	..
	25. ix	6	..	..	..	..	..	6	..	..	..
	9. x	7	..	..	..	..	..	7	..	..	..
	23. x	..	..	..	..	..	..	..	..	..	..
	17. xi	2	..	..	..	..	..	2	..	..	..
	20. xi	6	..	..	..	..	..	6	..	..	..
	11. xii	6	..	..	..	..	3	3	..	..	..
VI ♀	12. ix	17	..	..	..	..	..	15	2	..	0·325
	25. ix	22	..	..	..	..	1	15	6	..	0·330
	9. x	23	..	..	..	..	..	21	2	..	0·328
	23. x	4	..	..	..	..	..	2	2	..	..
	17. xi	25	..	..	..	..	..	13	12	..	0·335
	20. xi	41	..	..	..	..	8	31	2	..	0·310
	11. xii	14	..	..	..	..	..	11	3	..	0·330
V	12. ix	17	..	..	..	..	9	7	1	..	0·300
	25. ix	3	..	..	..	..	..	3	..	..	..
	9. x	42	..	..	..	..	28	14	..	..	0·296
	23. x	13	..	..	..	..	9	4	..	..	0·294
	17. xi	8	..	..	..	..	4	4	..	..	..
	20. xi	27	..	..	..	..	26	1	..	..	0·282
	11. xii	10	..	..	..	..	..	10	..	..	0·310
IV	12. ix	2	..	..	..	2	..	..	..	..	..
	25. ix	6	..	..	..	..	6	..	..	..	..
	9. x	68	..	..	..	52	16	..	..	..	0·259
	23. x	24	..	..	..	12	12	..	..	..	0·265
	17. xi	25	..	..	..	15	10	..	..	..	0·262
	20. xi	28	..	..	..	24	4	..	..	..	0·254
	11. xii	8	..	..	..	..	8	..	..	..	..
III	12. ix	2	..	..	1	1	..	..	..	..	..
	25. ix	..	..	..	..	6	..	..	..	..	..
	9. x	87	..	..	28	59	..	..	..	..	0·234
	23. x	36	..	..	7	29	..	..	..	..	0·238
	17. xi	7	..	..	3	4	..	..	..	..	..
	20. xi	6	..	..	3	3	..	..	..	..	..
	11. xii	14	..	..	..	14	..	..	..	..	0·244
II	12. ix	5	..	5	..	..	..	..	..	..	..
	25. ix	7	..	1	6	..	..	..	..	..	..
	9. x	58	..	37	21	..	..	..	..	..	0·191
	23. x	58	..	27	31	..	..	..	..	..	0·196
	17. xi	10	..	8	2	..	..	..	..	..	0·188
	20. xi	5	..	5	..	..	..	..	..	..	..
	11. xii	30	..	17	13	..	..	..	..	..	0·194
I	12. ix	13	12	1	..	..	..	..	..	..	0·151
	25. ix	12	11	1	..	..	..	..	..	..	0·151
	9. x	183	183	..	..	..	..	..	..	..	0·151
	23. x	89	88	1	..	..	..	..	..	..	0·151
	17. xi	24	24	..	..	..	..	..	..	..	0·151
	20. xi	1	1	..	..	..	..	..	..	..	..
	11. xii	74	74	..	..	..	..	..	..	..	0·151

TABLE XVII. *CORYCAEUS ANGLICUS*. SIZE IN MM.

Stage	Date	No.	0·442–0·495	0·495–0·548	0·548–0·602	0·602–0·655	0·655–0·708	0·708–0·761	Median size
VI ♂	14. viii	3	..	2	1	..	..	..	..
	28. viii	20	..	14	6	..	..	..	0·535
	12. ix	59	..	26	33	..	..	..	0·552
	25. ix	15	..	7	8	..	..	..	0·550
	9. x	72	..	44	28	..	..	..	0·544
	23. x	126	1	84	41	..	..	..	0·539
	17. xi	60	..	33	27	..	..	..	0·546
	20. xi	100	..	78	22	..	..	..	0·537
	11. xii	26	1	21	4	..	..	..	0·536
VI ♀	14. viii	3	..	..	..	..	3	..	..
	28. viii	6	..	..	..	..	6	..	..
	12. ix	25	..	..	..	2	20	3	0·681
	25. ix	13	..	..	..	3	10	..	0·666
	9. x	63	..	..	..	7	50	6	0·686
	23. x	96	..	..	..	47	49	..	0·655
	17. xi	45	..	..	..	21	24	..	0·656
	20. xi	29	..	..	..	18	11	..	0·649
	11. xii	15	..	..	..	11	4	..	0·633

Table XVIII. Cruises of January 1947.

(Numbers of copepods per m.^{3})

	Cruise A (6–8 January)			Cruise C (17–18 January)	
Station No. ..	1	6	7	2	4
Position ..	50° 02′ N., 4° 22′ W. (= E 1)	48° 34′ N., 5° 13′ W.	48° 49′ N., 5° 23′ W.	49° 46′ N., 6° 00′ W.	49° 46′ N., 6° 34′ W.
Calanus finmarchicus	..	27	15	11	20
Pseudocalanus elongatus	86	52	29	87	42
Paracalanus parvus	121	34	53	66	71
Centropages typicus	2	..	..	..	..
C. hamatus	..	..	..	..	..
Temora longicornis	4	..	..	..	..
Metrida lucens	..	2	11	14	71
Acartia clausi	5	..	..	..	..
Oithona similis	141	263	229	95	144
Median size of *Oithona* VI, ♀ (mm.)	3·438	0·434	..	0·479	0·475
Median size of *Paracalanus* VI, ♀ (mm.)	0·772	0·810	..	0·890	0·875

Table XIX. Cruise of 26–27 June 1947

(Numbers of copepods per m.^{3})

	L 4	1	2	3	4	5	6
Position ..	50° 15′ N., 4° 13′ W.	50° 03′ N., 4° 30′ W.	49° 56′ N., 4° 45′ W.	49° 30′ N., 5° 03′ W.	49° 14′ N., 5° 20′ W.	49° 14′ N., 5° 53′ W.	49° 14′ N., 6° 12′ W.
Calanus finmarchicus	30	30	53	960	180	70	130
Pseudocalanus elongatus	3040	2060	2454	3780	1225	1250	965
Paracalanus parvus	360	130	134	1380	90	175	360
Centropages typicus	60	70	59	100	30	45	80
C. hamatus	10	..	7	600	110	40	90
Temora longicornis	226	740	440	800	40	20	15
Acartia clausi	1840	850	693	220	25	30	..
Oithona similis	9540	3700	3834	4020	900	1140	2150
O. nana	10	10	13	..	5	..	..
Median size of *Pseudocalanus* VI, ♀ (mm.)	0·847	0·815	0·830	0·826	0·895	0·844	0·850

Table XX. Cruise of 5–7 August 1947

(Numbers of copepods per m.^{3})

Station no. ..	1	2	3	4	5
Position ..	L 4	Eddystone	49° 30′ N., 4° 17′ W.	49° 3′ N., 4° 58′ W.	48° 40′ N., 5° 32′ W.
Pseudocalanus elongatus	3345	3780	565	3500	1865
Paracalanus parvus	1965	1320	270	1100	830
Centropages typicus	160	220	175	400	605
C. hamatus	95	20	25	..	..
Temora longicornis	590	40	10	..	10
Acartia clausi	2760	1280	80	140	65
Oithona similis	9040	9040	2915	4440	3840
Median size of *Pseudocalanus* VI, ♀ (mm.)	0·805	0·810	0·783	0·853	0·804

Station no. ..	7	8	11	12	13
Position ..	49° 5′ N., 3° 33′ W.	49° 35′ N., 2° 54′ W.	50° 4′ N., 2° 11′ W.	50° 4′ N., 2° 58′ W.	50° 4′ N., 3° 46′ W.
Median size of *Pseudocalanus* VI, ♀ (mm.)	0·802	0·805	0·805	0·810	0·812

A BIOLOGICAL STUDY OF *FUCUS VESICULOSUS* L. AND *F. SERRATUS* L.

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(Text-figs. 1–33)

CONTENTS

	PAGE
Introduction	439
Distribution of the fucoid vegetation	441
Germination	443
Growth rate	449
Measurement of growth	449
Growth-rate in *Fucus vesiculosus*	450
Growth-rate in *Fucus serratus*	451
Comparison of observed growth-rates with records from other areas	453
Morphological rhythm in frond development	455
Vesicle-formation in *Fucus vesiculosus*	465
Reproduction	470
Reproduction in *Fucus serratus*	474
Reproduction in *Fucus vesiculosus*	476
Defoliation	481
Depopulation	484
Repopulation	488
Fucus vesiculosus on cleared areas	488
Fucus vesiculosus on cut areas	490
Fucus serratus on cleared areas	493
Fucus serratus on cut areas	495
Conclusion	497
Summary	498
References	499
Appendix (Tables IX–XXXIV)	501

Introduction

Though the two common species of *Fucus*—*F. vesiculosus* and *F. serratus*—are perhaps the best known of British seaweeds, an investigation into growth-rate and longevity for utilitarian purposes has revealed information of a scientific nature which is worthy of record.

Marine algae have provided material for research with varied objectives. The record of it reflects the changing viewpoints common to other branches of botany. The foundation of knowledge of British marine algae was laid by the naturalists of a hundred and fifty years ago, but its value has been overlaid,

and in some respects obscured, by deflexion into phylogenetics, amplified by detailed inquiry into life cycles, with an emphasis on the light which such study might shed on problems of evolution. Ecological study of marine algae is of comparatively recent growth. Some careful investigation of restricted areas has been made, and modern text-books now tend to assess ecological data as an essential complement to description. Nevertheless, information on behaviour of a plant, and the rhythm of successive growth-phases through which it passes in the course of its life, apart from cytological life cycles, is rarely given.

An investigation has been conducted over a period of five years, with the object of eliciting information on the behaviour of the two fucoid species over a period of time. The methods adopted were those used, with modification in detail, by other algologists (Hariot, 1909; Lemoine, 1913; Nienburg, 1930; Hatton, 1932).

One of the methods employed was to clear certain areas on the shore, varying in extent from single-metre squares to broad strips 16 m. wide, running through the entire fucoid zone from top to bottom of the shore, and penetrating into the upper fringe of the sublittoral zone. The second method entailed the marking of selected plants *in situ*. The method of marking which proved most satisfactory was the attachment to the plant of numbered chicken- or hen-rings. Very small plants were marked by small celluloid tablets with a split into which the frond could be inserted.

A very short period of experiment revealed the high mortality-rate among seaweeds. From a batch of marked plants quite often 75 % had disappeared after an interval of only a few weeks. The use of large marked plants was of limited value because of the extensive frond-breakage which occurred, even if the plants were not carried bodily away. Very large numbers of plants had to be marked in order to secure data of statistical significance.

Use was also made of prepared concrete blocks placed on the shore (see Lund, 1936). The blocks needed a preliminary soaking in sea water for some time before they could be used with success.

Preliminary inquiry also showed that growth-rate varied with locality, and, to obtain complete data, three stations were selected: south Devon (Wembury, near Plymouth); the south-west corner of the Isle of Man; and a station on the west coast of Argyll. Localities varying in aspect and exposure were chosen on each station to give opportunity of comparing growth-rates under different conditions.

One of the authors (M.K.) is responsible for the data from the Isle of Man, the illustrations, and the compilation of the report. The other (M.P.) has carried out all the observations on the Devon and Scottish stations.

Acknowledgements are due from the authors to the Development Commission, and to the Ministry of Supply, who sponsored the larger investigation from which the facts recorded have emerged.

Collection of data from the Isle of Man was facilitated by the willing assistance of a large number of students in the University of Liverpool, to whom acknowledgement is due, in particular to Miss Marion Anderton who gave valuable help with the treatment of data. Miss Emily Clay, M.Sc., acted as full-time assistant to Dr Parke.

Distribution of the Fucoid Vegetation

The first point worthy of note which emerged from a comparison of the three areas is that the bathymetric levels of the fucoid zones on the three stations did not coincide.

The restricted area on which observations were made on the Devon coast carried a fucoid vegetation which lay wholly below mid-tide level, whereas a corresponding belt on the Manx and Scottish coasts was much broader and occupied the zone between H.W.N.T. and L.W.S.T.

The findings of the authors for the restricted area at Wembury are not wholly in agreement with the records of Colman (1933) and Evans (1947) for slightly different areas on the same beach.

Colman made four transects on Church Reef at Wembury, three of them radiating from a convenient central point and the fourth set at an angle with one of the other transects. Two of Colman's transects gave a distribution of the fucoid belt quite in keeping with the authors' findings, i.e., except in pools, the fucoid vegetation is confined below or just reaches up to the line of M.S.L. On these two transects, no *Pelvetia* or *Fucus spiralis* was present in any quantity.

On the other two transects, the upper limits of the fucoid zone came well above the line of M.S.L. Colman (1933, p. 462, fig. 13) assesses the limits of distribution of the components of the fucoid belt as follows: *Pelvetia*, from half-way between M.H.W.S.T. and M.H.W.N.T. to the extreme lowest level of H.W.N.T; *Fucus spiralis*, from M.H.W.N.T. down to 1 ft. below the extreme lowest H.W.N.T; *Ascophyllum*, from just below extreme lowest H.W.N.T. to a level half-way between M.L.W.N.T. and M.L.W.S.T; *Fucus serratus*, from M.S.L. down to L.W.S.T.

Evans (1947, p. 182, fig. 2) included the same area, Church Reef, Wembury, in a general survey of a larger area on the Devon coast with Plymouth as the centre. He claims a higher upper limit for *Pelvetia* and raises it to a level above E.H.W.S.T. The upper limit for *Fucus spiralis* is also raised to a level midway between M.H.W.N.T. and M.H.W.S.T. These levels are considerably higher than those found by Colman on his transects, and agree with the authors' findings on the Manx and Scottish coasts. Evans also raises the upper zone of the *Ascophyllum* belt to M.H.W.N.T. He states that the top of the *Laminaria* zone is exposed only at the deepest of neap tides on the Devon coast. Evans's survey shows clearly the alteration in level of various algal zones in relation to the

degree of shelter from wave action, though the alteration is not necessarily in the same direction for all species.

In comparing the zonation of the fucoid belt on areas so widely separated as Devon, the Isle of Man and the coast of Argyll, it is obvious that caution must be exercised in making comparisons when the degree of wave action on each area has not been ascertained. Unfortunately, there is no means of assessing the force of wave action. Nevertheless, the areas selected by the authors in the three stations covered a very wide range of variation in the exposure factor from full surf on a headland facing west to an almost land-locked inlet. On the Manx and Scottish stations, the upper levels of *Ascophyllum* and *Fucus vesiculosus* lie higher on the shore than is shown by any of the records for Wembury, or, indeed, for any of the Devon areas surveyed so far. The difference in level amounts to not less than two vertical feet.

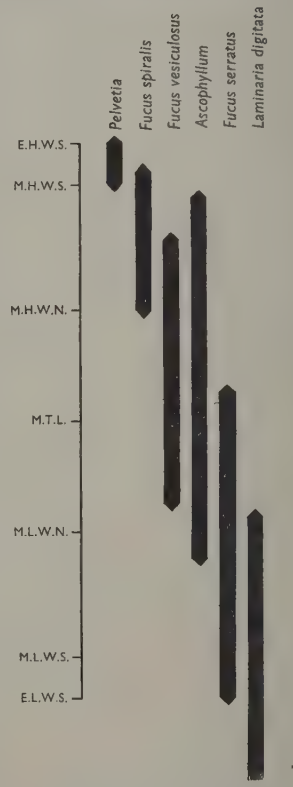

Fig. 1. The distribution of fucoids in relation to tidal level at Port Erin, Isle of Man.

The distribution of the fucoid zones on the Manx coast is shown in Fig. 1. It can be seen from the figure that *Pelvetia* lies at or, in sheltered places, above the level of E.H.W.S.T. and that *Fucus spiralis* reaches the M.H.W.S.T. level. *Ascophyllum*, accompanied by *Fucus vesiculosus*, reaches up to midway between M.H.W.N.T. and M.H.W.S.T. The distribution of *F. serratus* on the Manx coast appears to coincide with that on the Devon coast. Its upper level lies on M.S.L., but its lower limit lies in the fringe of the sublittoral zone. *Laminaria digitata* also appears to lie higher on the shore on the Manx coast when compared with the Devon coast. From Evans's records it would appear that the upper fringe of the *Laminaria* zone is exposed only by the deeper low waters of neap tides. On the Manx coast the highest *L. digitata* plants emerge at every low water level.

The relative alteration in level of the fucoid zones on shores of latitudes so far apart as Devon and the Isle of Man is to be expected. Tables for insolation and air humidity and the prevalence of mist or fog show that intertidal exposure on the south coast of Britain is likely to have more severe effects than in the north. The reduction in level of the plants on the south coast by

shortening the periods of exposure may compensate for the greater danger of desiccation.

Germination

The periods during which eggs are released from the plants are protracted for both species. Receptacles releasing gametes may be found in varying numbers somewhere or other on the shore for periods of 6 months for *Fucus vesiculosus* and 8 months for *F. serratus*. Receptacles in various stages of depletion may be found at other times when the egg supply falls to a minimum. The supply of eggs is enormous. Large plants may bear over 1000 fruiting apices, each carrying a large number of conceptacles in which egg development is maintained over a period. The largest number of receptacles recorded on single plants is 4678 for *F. serratus* and 3269 for *F. vesiculosus*. The number of eggs released by such large plants in the course of one fruiting season must be more than a million.

The large number of eggs produced is reflected in the large number of minute plants crowding the substratum below the larger plants. Table I records the number of young plants under 3 cm. in length growing on 1-metre-square experimental areas at Wembury. Both the original and final populations after clearance are recorded. The average proportion of young plants under 3 cm. in length, which may be regarded as indicative of the conditions for germination for each square, was 87·1 % for the original and 85·6 % for the final populations on *F. serratus* areas at Wembury. The proportion of such plants on the *F. vesiculosus* areas was somewhat less—74·1 % was recorded for the original and 57·4 % for the final populations.

From these results it would appear that the eggs of *F. serratus* have better opportunity for settlement and germination than those of *F. vesiculosus*. The range of variation in the data for the two species is from 28·2 to 98·9 % for *F. serratus* and from 15·2 to 95·2 % for *F. vesiculosus*. The discrepancy between the squares obviously reflects the physical conditions, because the total number of the plants in populations on the squares varies in parallel with the proportion of young plants.

The number of large plants in any area is affected by the degree of exposure of the area to wave action. *F. serratus* is more sensitive and the proportion of large plants in exposed places falls, thus making the proportion of young plants rise steeply. Conditions for germination may be good, but the rate of depopulation so high that the great majority of the plants may be less than 20 cm. in length. Port Erin Bay, on the Manx coast, faces west, and despite the partial shelter of a ruined breakwater, must be called an exposed coast. Data for the proportion of young plants in the population are given in Table II.

The records from Port Erin show some differences when compared with those from Wembury. The three strips were on a steeply shelving coast and subject to considerable battering by the waves. Metre-squares 8, 9, 19 and 20

on strip 1 sloped backwards towards the land and thus gained some shelter from the force of the waves. On these squares alone did the numbers of the

TABLE I. THE PROPORTION OF YOUNG PLANTS IN POPULATIONS ON 1-METRE-SQUARE EXPERIMENTAL AREAS AT WEMBURY

	Original population			Final population		
Metre sq. no.	Time of clearance	Total no. of plants	% under 3 cm. in length	No. of months of growth	Total no. of plants	% under 3 cm. in length
			F. serratus			
H 1	7. x. 41	8,163	87·9	35	5,471	95·4
2	6. xii. 41	634	28·2	33	1,761	47·3
3	15. vi. 42	3,978	90·5	27	1,837	81·0
L 1	6. x. 41	4,775	94·0	35	4,157	95·5
2	4. xii. 41	2,205	90·7	33	2,508	91·7
3	4. ii. 42	1,129	87·5	31	4,855	93·1
4	4. iv. 42	1,068	74·9	29	4,349	91·9
5	23. v. 42	7,056	93·5	28	2,271	79·2
6	14. vi. 42	4,934	97·3	27	9,373	97·3
7	13. vii. 42	2,970	97·5	26	8,022	96·7
8	15. viii. 42	2,594	93·8	25	400	60·0
9	11. ix. 42	7,651	95·5	24	1,635	80·8
10	9. x. 42	1,056	72·9	23	1,034	85·7
11	7. xi. 42	5,634	97·9	22	3,065	90·0
12	6. xii. 42	1,319	81·8	21	1,790	83·1
13	23. i. 43	1,019	95·7	20	6,863	92·6
14	17. ii. 43	1,004	87·6	19	9,668	89·0
15	26. iii. 43	1,361	88·1	18	12,858	91·3
16	21. iv. 43	5,664	98·8	17	5,263	84·3
	Total	64,214	Mean 87·1		Total 87,180	Mean 85·6
			F. vesiculosus			
1	5. ii. 42	317	66·6	30	11,589	95·2
2	7. iii. 42	—	—	29	(6,669)	(90·2)
3	13. iv. 42	1,159	69·0	29	1,991	76·3
4	13. v. 42	4,786	91·9	28	5,720	85·1
5	16. vi. 42	1,583	83·1	27	1,574	74·3
6	14. vii. 42	1,153	76·3	34	3,997	80·0
7	13. viii. 42	1,827	90·8	33	2,316	92·4
8	10. ix. 42	3,837	91·2	32	646	49·5
9	8. x. 42	1,259	73·0	31	345	46·4
10	6. xi. 42	1,698	87·1	30	405	19·8
11	5. xii. 42	1,289	71·3	29	629	19·0
12	20. i. 43	1,608	72·7	28	1,415	48·0
13	18. ii. 43	902	88·7	27	699	51·5
14	24. iii. 43	721	44·3	26	1,365	49·3
15	20. iv. 43	1,617	64·3	25	1,044	15·2
16	22. v. 43	1,776	40·5	24	1,161	58·5
	Total	25,532	Mean 74·1		Total 34,896 (less sq. 2)	Mean 57·4

F. serratus: 1-metre-square areas all re-cleared in September 1944. H = top of *Fucus serratus* zone; L = lower part of the *F. serratus* zone.

F. vesiculosus: Nos. 1–5 areas re-cleared August–September 1944. Nos. 6–16 areas re-cleared April–May 1945.

population approach those for the Wembury area. On the other squares the difficulty in settlement of the eggs is shown by the small numbers of plants in

Table II. The Proportion of Young Plants in Populations on 1-metre-square Experimental Areas at Port Erin

Strip 1. *Fucus serratus* and *F. vesiculosus*

Metre sq. no.	Total no. of plants	% under 10 cm. in length
1	124	41·1
2	847	94·6
3	962	93·7
4	332	70·2
5	788	92·5
6	660	48·9
7	310	98·3
8	1166	98·9
9	2168	99·2
10	421	93·5
11	393	82·9
12	243	83·1
13	597	93·8
14	907	92·1
15	957	88·1
16	876	81·3
17	904	84·2
18	1286	63·6
19	755	88·1
20	1150	87·6
21	433	79·4
22	636	92·6
23	720	87·1
24	381	82·4
25	14	21·4
26	27	88·5
27	47	29·7

Strip 2

	Original population		Final population			
			F. vesiculosus		*F. serratus*	
Metre sq. no.	Total no. of plants	% under 10 cm. in length	Total no. of plants	% under 10 cm. in length	Total no. of plants	% under 10 cm. in length
11	68	39·7	214	85·5	125	46·4
12	12	0	188	21·2	161	90·1
13	3132	98·8	614	84·3	481	58·2
14	981	96·1	214	85·5	700	65·8
15	—	—	2	0	626	75·1
16	1637	97·6	—	—	1194	62·8
17	4615	98·3	218	82·1	1114	60·1

Strip 3

	Final population	
Metre sq. no.	Total no. of plants	% under 10 cm. in length
13	1248	31·2
14	866	22·1
15	1110	10·2
16	1212	44·2

Note: Strip 1. Original clearance August 1941.
Strip 2. Original clearance April 1942; re-cleared September 1944.
Strip 3. Original clearance August 1942; re-cleared September 1944.

the populations. The depletion factor is also very high and varies from square to square, so that the range of proportions of plants under 10 cm. in length on the various squares is from 21·4 to 99·2 %.

Strips 2 and 3 were taken across a sharp ridge. Metre-squares 13 and 17 on strip 2 and all four metre-squares on strip 3 lay at a lower angle than the other squares, and the better conditions for settlement are reflected in the larger populations on these squares.

Eggs are sown broadcast over the shore and begin development wherever they fall, even in places where further growth will be impossible. The egg becomes attached to the rock within a few hours of settlement and may adhere firmly enough to the substratum to resist removal by the next returning tide.

An enormous number of eggs are, doubtless, washed away. Many more fall a prey to browsing molluscs, especially limpets and species of *Littorina*; but, even discounting these risks, there is a sufficient supply of attached eggs to replace plants removed from the population by accident or old age.

Estimation of the time required for the development of a fertilized egg into a visible germling was made by clearing small areas on the shore by a method which ensured the destruction of all eggs and microscopic germlings. This was done by one of three methods: exposing the rock surface, roughly cleared by scraping, to the action of a blow-lamp; by chipping off the surface rock to expose a new surface; by laying down blocks of prepared concrete. After each of these treatments experiment shows that colonization is rapid. From Table III it is seen that the time required for re-establishment of minute plants after all eggs and germlings had been removed does not differ greatly from that required when the surface was merely scraped.

The experimental area on the Manx coast was cleared in August 1941, but there was no opportunity of examining it until December, 100 days later. Consideration of the data provided by the first inspection of the area shows that the time required for germination of the eggs was not dissimilar to that given for the Wembury plants (Tables III, IV, V).

From the foregoing, it may be assumed that growth of the germling is continuous from the time it settles on the substratum, and that it may be visible to the naked eye within 2 weeks of settling.

The experimental areas covered every level at which the two species appear on the shores. There does not appear to be any level which is particularly favourable to settlement of eggs. The differences in settlement in various metre-squares on the areas are not due to difference in level, but they may be due to difference in the texture of the surface of the rock or to the slope of the substratum. Local increase in angle of slope enhances the difficulty in settlement of eggs; a smooth rock surface and absence of cracks is also a deterrent. This is clearly shown by the fact that the earliest and most rapid development of young plants takes place in cracks and fissures in the rock surface.

Germination of eggs of *Fucus serratus* is likely to be more uniform at all levels than that of *F. vesiculosus*. The higher level at which the latter species grows exposes the eggs to a greater range of inimical physical factors. Light

TABLE III. RECOLONIZATION OF *FUCUS SERRATUS* AFTER CLEARANCE ON THE ARGYLL AND DEVON COASTS

Experimental area	Method of clearance	No. of days after clearance	Maximum size of germlings in cm.
Argyll:			
Serratus Rock	Scraping	41	1·0
Ascophyllum Rock, E. strip	Scraping	41	3·0
Devon:			
Strip sq. 14	Rock surface removed	58	5·2
Strip sq. 15	Cleared by blow-lamp	47	1·1
Strip sq. 19	Rock surface removed	38	1·0
Strip sq. 19A, 2	Rock surface removed	175	2·0
F.S.L. 1	Scraping	59	2·0
6	Scraping	71	4·0
7	Scraping	42	3·0
8	Scraping	28	1·5
9	Scraping	58	3·0
10	Scraping	64	3·5
11	Scraping	64	3·5
12	Scraping	49	2·0
13	Scraping	27	1·0
14	Scraping	31	1·0
15	Scraping	26	1·5
16	Scraping	30	3·0

TABLE IV. RECOLONIZATION OF *FUCUS SERRATUS* AFTER CLEARANCE AT PORT ERIN ON THE MANX COAST

Experimental area	Method of clearance	No. of days after clearance	Maximum size of germlings in cm.	
			Range	Mean
Strip 1, metre sq. nos. 10–23	Scraping	100 ± 4	3·0–14·0	9·4
Strip 2, metre sq. nos. 12–15	Scraping	101	6·0–16·0	8·8
Strip 3, metre sq. nos. 1–2	Cleared by blow-lamp	54	0·5– 1·0	0·8

TABLE V. RECOLONIZATION OF *FUCUS VESICULOSUS* AFTER CLEARANCE ON THE DEVON AND MANX COASTS

Experimental area	Method of clearance	No. of days after clearance	Maximum size of germlings in cm.	
			Range	Mean
Wembury, metre sq. nos. 5–16	Scraping	28 ± 14	1·0– 3·0	1·5
Port Erin, strip 1, metre sq. nos. 1–7	Scraping	101 ± 1	3·0–10·5	6·0

favours germination; hence a greater population of small plants in the upper levels of the *F. vesiculosus* zone might be expected. It is a fact that on coasts where the *F. vesiculosus* zone lies high on the shore, as on the Manx coast, the upper edge of the zone carries a dense carpet of young plants, without any larger plants. The factor of desiccation appears to work in contrary direction to

that of increased illumination, with the result that, though germination may be easy in the upper levels of the belt, further growth is difficult where the periods of exposure are great relative to those of submergence. The result of these two opposing factors on the Manx coast is the maintenance of a dwarf population at the top level of the zone, where the plants remain in a condition of protracted juvenility. An area of plants in this position was kept under observation for 2 years. The plants were 2–3 cm. long and remained at that length for the whole period. That they were still alive was demonstrated by the fact that when the boulder on which the plants were growing was removed to a lower level on the shore in the *F. vesiculosus* zone, the plants began to elongate at once, and within 3 months had reached a length of 9 cm. Their further progress in the new position was quite normal.

On shores sloping towards the south in the Isle of Man, and frequently on the Devon coast near Plymouth, no germlings appear on a cleared area until after a carpet of *Enteromorpha* or *Ulva* has developed as a cover to the rock surface. The most vulnerable early stages of germination thus take place under the *Enteromorpha* carpet, and, by the time the tips of the germlings project above it, they are strong enough to resist desiccation and the depredations of molluscs. Hatton (1932), working at St Vaast-la-Hougue, found the same interaction between *Enteromorpha* and *Fucus* germlings. In this more southerly station, Hatton found that a carpet of *Enteromorpha* was almost an essential condition for good germination of *Fucus* eggs, and that the latter were noticeably fewer where the *Enteromorpha* did not develop. Normally, of course, on an uncleared area, the eggs develop under cover of the adult population, which provides adequate protection from desiccation and reduces the risk of destruction by molluscs.

The influence of increased light after clearance of the original population from an area might have been expected to facilitate germination of eggs and lead to a denser population on the experimental areas. This hypothesis has been borne out by experiment. Reference to Table I will show that the final population on the Devon coast was larger than the original population for both species of *Fucus*. The total original population figures for a series of 16 squares, each 1 metre square, are: *F. serratus* 64,214, *F. vesiculosus* 25,532; the numbers in the final populations were: *F. serratus* 87,180, an increase of 36 %, and *F. vesiculosus* 34,896, an increase of 37 %. The data for the Isle of Man showed an increase of 9·8 % for the final population of *F. serratus*. The figure for *F. vesiculosus* would have been much higher. There was an obvious increase in density of population on the experimental squares, but final analysis was prevented by a storm which covered the experimental area with a pile of boulders.

It is probable that *F. vesiculosus* and *F. serratus* would extend their natural boundaries in the absence of mutual competition. Experiments have shown that areas cleared artificially or accidentally in one zone may be

colonized by plants proper to another zone. The intruders may persist for a year or longer but will eventually be driven out by competition.

In latitudes more northerly than those investigated by the authors, *F. serratus* may rise higher on the shore and has been found on the upper levels in the Orkney Islands. There are also references to *F. serratus* at fairly high levels on the south coast of England, but in these circumstances the plants come early into the fruiting stage and die out within a year.

Larger plants are found distributed over the zone at all levels except the extreme upper limits. The best population is found in the middle region where a mixed population of all sizes develops. It is possible that the light factor controls the lower limit of *F. vesiculosus* on the Devon coast, compared with that in higher latitudes. The claim that light is the determining factor was made by Gail (1918). The lower position of *F. serratus* relative to that of *F. vesiculosus* may indicate a greater tolerance of reduced light and/or a greater intolerance of exposure to the drying action of the atmosphere.

Growth-rate

Measurement of Growth

Two methods were employed to determine growth-rate. The first was to clear an area of its population and then record the sizes of plants in the new population at intervals. Two difficulties immediately became apparent. Eggs from plants in the vicinity of the experimental areas are shed continuously over a long period; later, when the short sterile period approaches, the egg output falls but may not fail completely. The result is that the experimental areas are almost continuously resown with eggs after the experiment has started. The new population on the areas is thus of different ages. Records were made at intervals of the length of the longest plants, on the assumption that the longest would be the oldest in a population of young plants of all sizes, down to just visible germlings. The assumption that the longest plants were the oldest is not necessarily justified because the germlings possess, as is common to seedlings of higher plants, great variation in individual vigour. It is difficult to explain the precocious advance in length of some germlings relative to others on any other grounds. It may be stated, however, that competition may play a part in the early stages of growth, because isolated germlings usually showed higher growth-rate than those which were crowded together; germlings which developed in cracks in the rock also seemed to gain an advantage from their position.

The second difficulty was the very rapid depopulation-rate. Serial records of maximum size sometimes showed a decrease, because the largest germlings had been removed by some agency or another in the interval between the observations.

The other method used was to mark individual plants and to measure

them at intervals. Here, again, the ease with which plants are broken and the longest fronds removed by rough water or the depredations of molluscs proved a hindrance. This difficulty naturally increased as the plants grew longer.

Increase in length appears to be a uniform process for young plants of both *F. vesiculosus* and *F. serratus* during their first year, irrespective of the time of year at which they start life. This fact was established by clearing metre squares at intervals of 1 month to cover a whole year. Inspection of older plants suggested that there might be an alternation of periods of vegetative growth and reproductive periods in which extension of the frond was reduced. Serial records of growth through the reproductive period does not, however, bear out this hypothesis. The impression is given by the fact that as the reproductive fronds wear away they leave the new vegetative frondage in full view and very conspicuous by the lighter colour of the frond tips.

Elongation alone is, of course, no full measure of growth. Dichotomy of the fronds and development of lateral frondage goes on simultaneously with linear extension. An attempt was made in some of the experiments to record the degree of 'bushiness' by counting the number of frond apices at the times when their length was recorded. In this feature plants showed individual variation, some developing dichotomies in lateral frondage more vigorously than others. An example of the degree of branching is given in Table IX in the Appendix (p. 501). Plant A4 showed an increase in the number of frond apices from 16 to 1777 in a period of 377 days, during which it increased in length from 21·0 to 61·0 cm. This plant was evidently a very vigorous specimen because the increase in length in one year was 39·0 cm. compared with the normal yearly extension of 22·4 cm. It was impossible to count the frond apices on all the experimental plants, and as normal extension of frond branching was concomitant with extension, the elongation factor was used as a criterion for growth.

Growth-rate in Fucus vesiculosus

Observations on frond extension were made in all three areas using the methods of cleared areas and marked plants (Tables IX–XVII, pp. 501–4).

The experiments in the Isle of Man (Table XV) were brought to a premature conclusion by the incidence of a heavy gale in April 1943, during which the experimental strip was buried under piles of large stones to a depth of several feet and many of the boulders under observation were removed bodily. Data from the Isle of Man, therefore, refer only to a period of 1 year and 9 months. From the data it has been determined that an average growth-rate of 0·45 cm. per week is maintained by *F. vesiculosus*.

Growth-rate data from Wembury are obtained from a large number of plots selected from all levels and under varying conditions of exposure in the *F. vesiculosus* zone (Tables IX–XIV). A summary of the results from Wembury

is contained in Table VI. The variation in growth-rate from the individual plots is from 0·25 to 0·71 cm. per week. The average rate from twenty-eight separate plots is 0·48 cm. per week. This figure agrees reasonably well with the average growth-rate of 0·45 cm. per week for the Manx plants, bearing in mind that the Devon plants had a longer period in which to grow. It has been established that the growth-rate in the second year and succeeding years may be slightly higher than that for the first year.

TABLE VI. RATE OF GROWTH IN LENGTH IN *FUCUS VESICULOSUS* ON THE EXPERIMENTAL AREAS ON THE DEVON COAST

Experimental area	No. of sites	Growth-rate per week (cm.) Min.	Max.	Mean
F. vesiculosus area	6	0·25	0·63	0·42
Strip, sqs. 14 and 16*a*	6	0·43	0·71	0·55
F. vesiculosus metre sqs.	16	0·32	0·57	0·47

Average growth-rate on 28 sites, 0·48 cm. per week.

The rate of elongation of the Scottish plants showed considerable variation (Tables XVI, XVII). The range of exposure on the individual plots in the Scottish station was very wide and the records show the effect on the growth-rate. On the very exposed plot on Sgeir Bhuidhe the rate of elongation for *F. vesiculosus* was, on the average, 0·31 cm. per week, a value which is less than that for growth-rate of *F. vesiculosus* on the Manx and Devon coasts. On the other hand, growth-rates for the other plots on the Scottish station showed much higher values. The Ascophyllum Rock plot which was in a sheltered locality gave a growth-rate of 0·68 cm. per week, a value which is much higher than the average for *F. vesiculosus* on any other station.

Breakage on exposed coasts is higher than in sheltered localities, and the recorded interim lengths may well be less than the real lengths, but a sufficient number of plants escaped breakage to establish the principle that the rate of growth in exposed places is actually slower than in sheltered localities.

Growth-rate in Fucus serratus

Comparison of the data from the three stations showed considerable variation in growth-rate. On the Devon coast a large number of marked plants were studied, as well as cleared areas. The data from these experiments are given in Tables XVIII–XXVII in the Appendix (pp. 505–10). Summarizing the data from the Devon coast, it may be stated that the average elongation rate for *F. serratus* from all sources was 0·49 cm. per week with a range of variation of 0·31–0·71 cm. per week. The value 0·49 cm. per week is very close to that found in the same area for *F. vesiculosus*, but the range is slightly more restricted than for the latter species, viz. 0·48, range 0·25–0·71 cm.

Three areas were examined on the Manx coast. Three strips were cleared in Port Erin Bay. Strip 1 ran down on a fairly steep coast from H.W.N.T. to

E.L.W.S.T., passing through the entire fucoid zone. Squares 10–27 ran through the *F. serratus* zone. Table XXVIII in the Appendix gives the details of observations on this strip. The elongation-rate is slightly reduced in the extreme upper and lower levels, but is fairly uniform throughout the greater part of the strip. The average growth-rate is 0·57 cm. per week, with a range of 0·43–0·65 cm. per week. The period of the experiment was 2 years and 9 months. Two other shorter strips alongside strip 1 gave average rates of 0·58 and 0·68 cm. per week, with ranges of 0·53–0·63 and 0·65–0·70 cm. per week respectively.

The other two Manx areas lay on the south-east coast at Port St Mary and Castletown (Table XXIX). The growth-rates from these two areas gave rather higher values than those from the Port Erin area. Average values of 0·73 (Port St Mary) and 0·84 (Castletown) cm. per week were obtained.

This variation in growth-rate appears to be correlated with the degree of shelter from direct wave action on the three areas. Port Erin Bay with a steeper coast, facing west, experiences considerable battering by the waves, driven by prevailing westerly winds. Port St Mary and Castletown lie on that part of the coast where the tide runs parallel with the land. The coast is also formed of very gently inclined terraces of limestone, and the waves tend to roll over the shore rather than impinge with battering force against it. The breakage factor on the Port Erin shore is likely to be greater than on either of the other two Manx stations, and it is probable that the observed average elongation-rate here falls rather further below the real elongation-rate than on the sheltered areas. There is, however, other evidence that the growth-rate on the protected areas is really greater than that on the exposed shore at Port Erin. Not only is the maximum length of plants normally greater in the sheltered areas, but the internodes between forkings are also longer. It must be admitted that the records from the two stations on the sheltered coast were drawn from observations over a period of 1 year only, but comparison of normal populations from the three areas supports the view that growth-rate rises with increasing shelter.

It must be pointed out that the lowest growth-rate recorded for the Isle of Man, even on the exposed coast, exceeds that for the Devon plants and suggests that a higher latitude with reduced inimical factors operating during periods of exposure may also have a beneficial effect on growth-rate.

This hypothesis is borne out by the fact that the highest growth-rates for *F. serratus* come from the Argyll coast (Tables XXX, XXXI). The various plots on the Scottish coast give a range of elongation-rates from 0·56 to 0·91 cm. per week for three stations, but the range of variation for plots and marked plants within each area is from 0·15 to 1·82 cm. per week. The Serratus Rock station was specially chosen because of the luxuriant growth of *F. serratus* in the original population. The average growth-rate on this station was 0·90 cm. per week for cleared areas and 0·91 cm. per week for marked plants. This

gives a rate for the Scottish plants which is nearly double that of the Devon plants. The greater growth-rate is also accompanied by greater internode length.

A summary of recorded growth-rates for *F. serratus* from all sources is given in Table VII.

TABLE VII. RATE OF GROWTH IN LENGTH IN *FUCUS SERRATUS* ON THE EXPERIMENTAL AREAS ON THE DEVON, MANX AND ARGYLL COASTS

Experimental area	No. of sites	Growth-rate per week (cm.) Min.	Max.	Mean
Devon:				
Strip, sqs. 15–22	19	0·31	0·71	0·48
F. serratus metre sqs.	19	0·41	0·63	0·53
Average growth-rate for 38 sites, 0·49 cm. per week.				
Isle of Man:				
Port Erin, strips 1–3	26	0·43	0·70	0·59
Port St Mary	5	0·58	0·90	0·73
Castletown	5	0·74	1·04	0·84
Average growth-rate for 36 sites, 0·68 cm. per week.				
Argyll:				
Serratus Rock	11	0·72	1·10	0·93
Ascophyllum Rock	3	0·47	0·66	0·57
Average growth-rate for 14 sites, 0·85 cm. per week.				

COMPARISON OF OBSERVED GROWTH-RATES WITH RECORDS FROM OTHER AREAS

A very wide range of growth-rate is given for *F. vesiculosus* and *F. serratus* from other areas. On the French coast, Lemoine (1913) records from Roscoff a growth-rate for *F. vesiculosus* of 2·5–3·3 cm. per month. The period of experiment was short, but if the rate had been maintained over a longer period it would have given a slightly higher rate than that found for *F. vesiculosus* on British coasts. The same is true for *F. serratus*. Lemoine records an increase in length of 12 cm. in 2 months, which is a much higher growth-rate than is shown on British coasts. Records from other French stations show slower rates. Hatton (1932) records elongation-rates from St Servan of 9·8–13·3 cm. in 7 months. This would give a weekly elongation of 0·31–0·47 cm., a rate comparable with those of British plants. Hariot (1909) records growth-rates of 4·5 cm. in 8 months for *F. vesiculosus* and *F. spiralis* from St Vaast-la-Hougue. This rate is low and may possibly be attributable to peculiar factors of the environment.

Results from other areas show slower growth-rates. Nienburg (1930) reports an average length of 20–25 cm. per year for both species. Furthermore, Lund (1936) quotes growth-rates of 4–6 cm. per year for the Danish coast and illustrates a plant which measured only 14 cm. at the end of 3 years. Records from the Norwegian coast at Trøndelagen (Printz, 1926) give growth-rates of

4–7 cm. per year, but Gislén (1930) records for the Gullmar Fjord on the Swedish coast a growth-rate of 6–14 cm. in 7 months. In extreme northern waters the effect of reduced light has to be considered, as little growth takes place in the dark winters.

The effect of changing salinity may also have an effect on growth-rate. It certainly affects the form of the plant, usually by causing dilatation of the receptacles, and may also affect growth-rate. Colman quotes the work of Segerstråle from Finland in water with a salinity of 4 $^{o}/_{oo}$ and a very small tidal range, in which the author records plants of *F. vesiculosus* which reached a length of 2–3 m. Such a great length has not been equalled by any of the plants which came under observation in the course of the present survey,

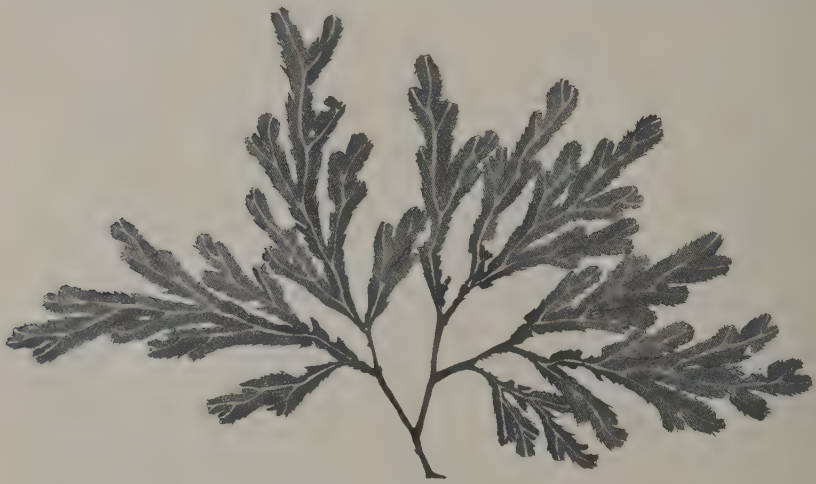

Fig. 2. Sterile plant of *Fucus serratus* from the Devon coast just over 1 year old. ×0·22.

though old plants of *F. vesiculosus*, consisting of twisted defoliated strands of more than 1 m. in length, are frequently met with in sheltered places.

Rees (1932) is of the opinion that aeration of the water plays a determining part in the development of both *F. vesiculosus* and *F. serratus*. He reports that at Lough Ine, on the south-west coast of Ireland, *F. serratus* occurs only in the almost land-locked lough at stations where the tidal current moves with its greatest rapidity.

The greatest contrast in growth-rate found by the authors is between plants of *F. serratus* at Wembury and on the Argyll coast. Fig. 2 shows a plant of *F. serratus* from the Devon station in its second year. This should be compared with Fig. 3, which represents a plant from the Argyll station in its first year.

Morphological Rhythm in Frond Development

Dichotomy of the frond takes place repeatedly, thus dividing it into sections which may be called, for convenience, 'internodes'. In a young plant the first internode is commonly longer than those which follow. On a growing frond the youngest internodes are naturally shorter than in the older ones, but even

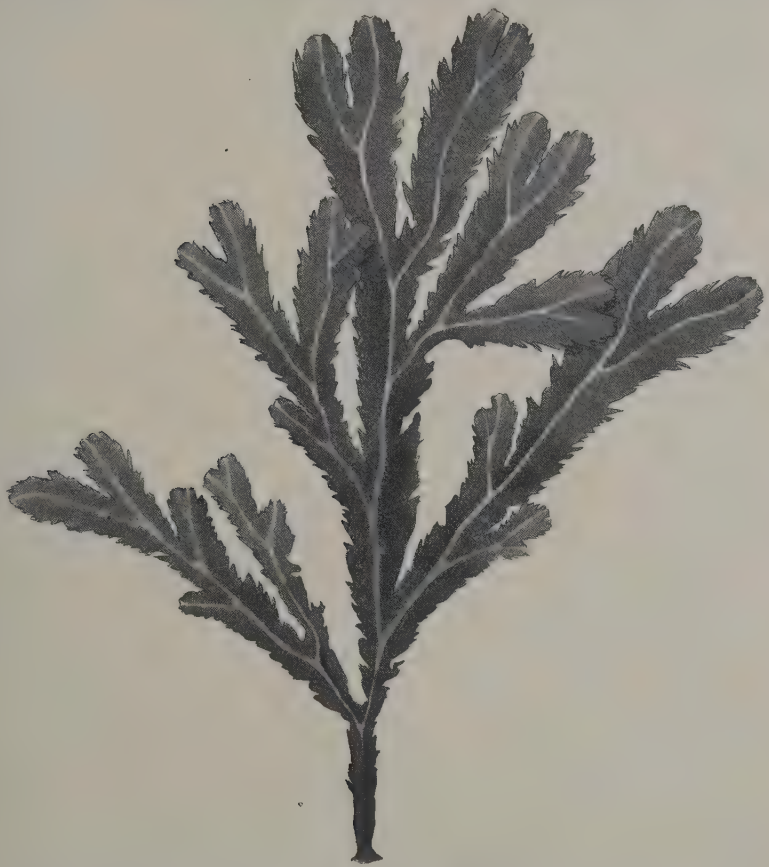

Fig. 3. Sterile plant of *Fucus serratus* from the Argyll coast in its first year. ×0·25.

mature lengths of internodes vary considerably. The variation in internode length is not so marked in the first year, but as the plant approaches reproduction, those fans that are destined to bear receptacles are forked at short intervals.

When an internode is delimited by apical dichotomy, it may have reached only 40–50 % of its final length. Subsequent elongation is brought about by

secondary tissue-formation and by swelling of internal cell-walls. The secondary extension diminishes in rate with the passage of time and finally ceases. As a plant grows larger, the basal internodes thicken to form a stipe. The thickening is accompanied by a secondary shortening of internodal length, which may amount to 18 % of the original (maximum) length. Progressive thickening of the midrib portion, accompanied by denudation of the wings of the frond, begins at the first internode and moves acropetally, affecting in turn all fronds but those most recently formed.

When the number of dichotomies is plotted against frond-length the result shows an almost straight-line relation, but the graph loses form somewhat with larger plants from which much of the frondage may have been lost. The rate of forking relative to length has been found to vary considerably for both species between the three stations.

Variation in dichotomy/length relation for *F. vesiculosus* on all stations is shown in Fig. 4. The Manx plants show a greater rate of forking than the Devon plants. Manx plants would have fourteen and Devon plants nine dichotomies for a length of 60 cm. Plants of *F. vesiculosus* from the Sgeir Bhuidhe area on the Argyll coast did not reach a length of 60 cm. The longest recorded was only 40 cm., but even so, had twenty-three dichotomies. The data from the other Scottish areas are not sufficiently numerous to permit of analysis of length to dichotomy but appear to lie very near to those for the Devon plants.

The extraordinarily rapid rate of dichotomy in plants from the Sgeir Bhuidhe area, and the fact that the dichotomy rate on the Manx coast was highest in Port Erin Bay suggests that one effect of exposure to rough water may be to accelerate dichotomy. The Sgeir Bhuidhe station is very exposed and so is Port Erin Bay. Both areas are also on steeply shelving coasts. The increase in rate of dichotomy is also accompanied by decreased growth-rate.

The rate of forking in *F. serratus* shows an even more marked variation from one station to another (Fig. 5). The number of dichotomies relative to length is highest in plants from the Devon station. The rate of forking on the Manx coast is less rapid but varies with the degree of shelter. A plant of 60 cm. in length would have thirteen dichotomies on the Manx coast and nineteen on the Devon coast. Scottish plants have still longer internodes, that is, the rate of forking is much slower even than in the Manx plants. Plants 60 cm. in length from the Ascophyllum Rock station would have only eleven dichotomies, and those from the Serratus Rock plot would have only nine dichotomies.

It is clear that rate of forking and elongation-rate are correlated inversely with one another. The more slowly a plant grows, the more rapidly it forks. It appears probable that in both species a reaction to inimical conditions is shown by retarded growth-rate and increased forking. Despite this variation in response to local conditions, especially degree of shelter, there is no doubt that there is an over-all increase in growth-rate and a marked diminution in the

rate of forking as one moves from the south coast, via the Isle of Man, to the Argyll coast.

After a dichotomy has been established, the two arms develop into frondage, but at very different rates. One arm has the advantage and grows more quickly than the other arm (Figs. 6, 7A). Examination of an old frond may show that more than two-thirds of the total frondage has been developed from one

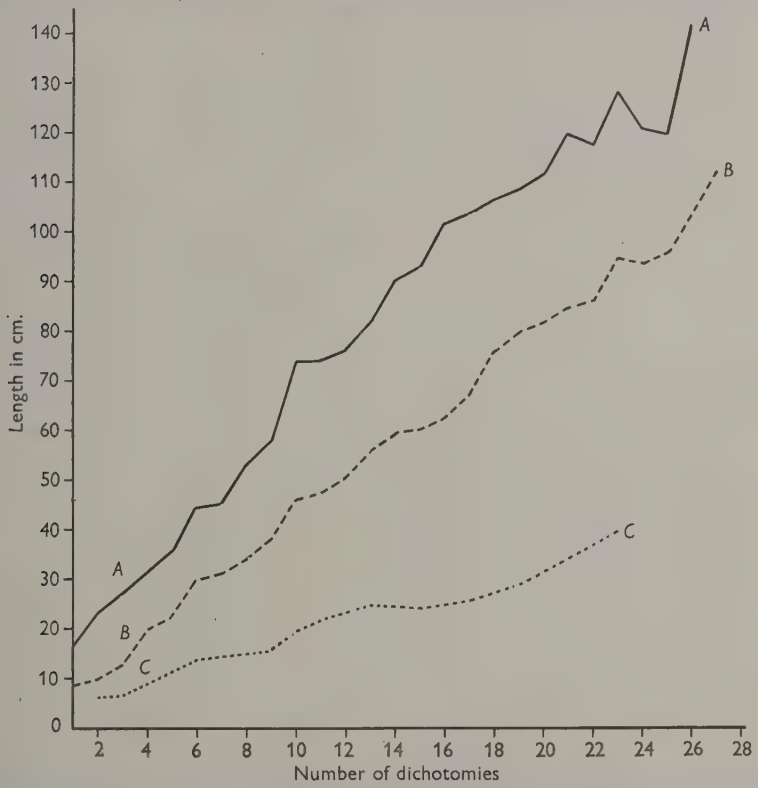

Fig. 4. Length to dichotomy relations in *Fucus vesiculosus* on the Devon, Manx and Argyll coasts. *A*, Church Reef, Wembury, Devon; *B*, Port Erin, Isle of Man; *C*, Sgeir Bhuidhe, off the west coast of the island of Luing, Argyll.

arm of the first dichotomy. Occasionally, in *F. serratus* and more rarely in *F. vesiculosus*, the rate of development of the two arms of the first dichotomy is approximately equal and a 'twin-thallus' is formed. This is seen in *F. serratus* in Fig. 7B. Fig. 10 shows an almost similar condition for *F. vesiculosus*.

If the dichotomies are followed in sequence along the length of a frond, it will be seen that the emphasis of development of one arm of a fork compared

with the other shows regular alternation from side to side of the frond. This overgrowth of alternate arms of a fork at successive dichotomies appears to be a fundamental morphological feature of both species, though it is more strictly maintained in *F. serratus* than in *F. vesiculosus* (Figs. 8, 9).

This inequality between the two arms of a fork is obviously due to a difference in growth-potential between the products of division of an apical cell. It suggests that the division of the apex is not a true dichotomy, as it is, for

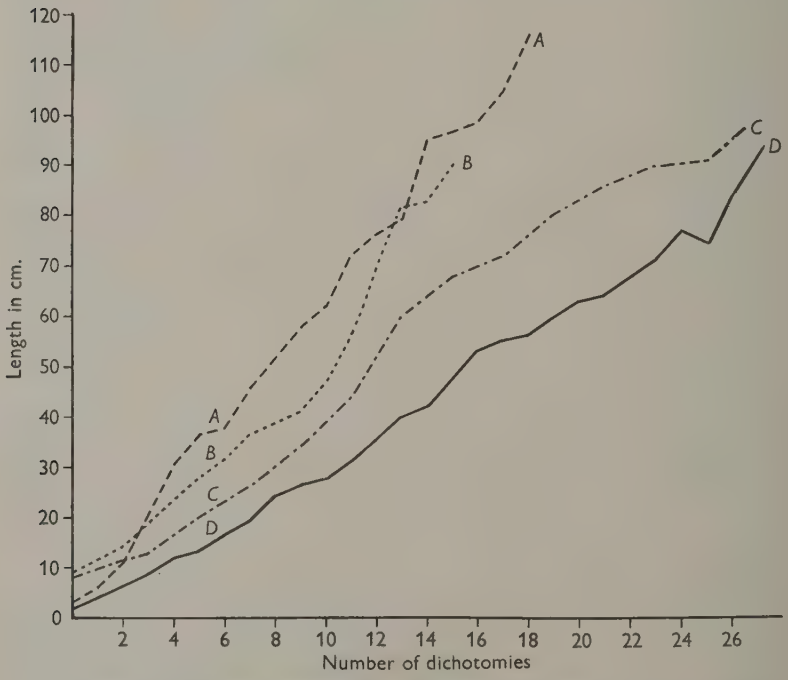

Fig. 5. Length to dichotomy relations in *Fucus serratus*. *A*, 'Serratus Rock', off the west coast of the island of Luing, Argyll; *B*, 'Ascophyllum Rock', west coast of the island of Luing, Argyll; *C*, Port Erin, Isle of Man; *D*, Church Reef, Wembury, Devon.

example, in *Dictyota*, but that one arm of the fork is due to the activity of a segment cut off from the apical cell which itself serves as the growing point for the other arm of the fork. The inequality of growth-potential would be explained by the excess of vigour of the original apical cell over the segment, to the activity of which the lesser arm of the fork is due. The alternation of excess growth-potential is therefore only an effect of regular segmentation from alternate sides of an apical cell.

On this view the two species of *Fucus* under discussion might be regarded as having a monopodial rather than a dichotomous habit of branching, but it is a monopodial system in which the lateral branch initial arises in the immediate vicinity of the apical cell and thus simulates a dichotomy. This method of unequal development of the two arms of a fork is, of course, carried to much greater degree by members of allied families as, for example, the Sargassaceae.

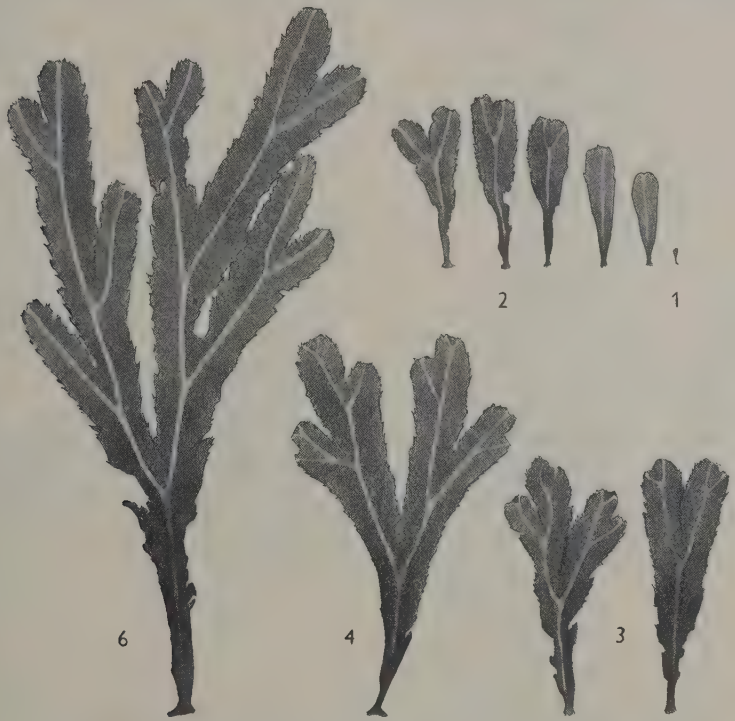

Fig. 6. Germlings of *Fucus serratus* from 1 to 6 months in age. ×0·27.

Not only is there an unequal capacity for frond development between the two arms of a fork, but the fate of the frondage developed from the arms may also differ. For example, in *F. vesiculosus* that arm of a fork which has the lower growth-potential usually forms a reproductive fan, forked at short intervals and forming receptacles at the tips of the fronds (Fig. 10). The other arm grows forward as a 'leader' and may give off *seriatim*, left and right, other reproductive fans. Occasionally one or two apices on the younger reproductive fans may remain sterile and act as secondary 'leaders', repeating the behaviour of the primary 'leaders' and adding to the bushiness of the plant.

At the time of fruiting, both primary and secondary leaders may be observed projecting beyond the general periphery of the frondage (Fig. 10). It may be noticed that receptacle development has been imposed simultaneously on lateral fronds of different ages. The basal older ones have undergone the greater number of dichotomies and bear the larger number of receptacles. The fruiting fronds will be ultimately removed after fruiting, and the leaders will

Fig. 7. *Fucus serratus* plants from the Manx coast showing normal form (A) and 'twin thallus' form (B). ×0·23.

grow forward to produce new distal frondage, with the result that no frondage is left on the proximal part of the plant, except where proliferation may give new frondage from old midribs. The basal part of an old plant, therefore, consists of a tangle of midribs from which the wings have been denuded, beset with spines to mark the places of excised fruiting fronds.

In the development of its frondage, *F. serratus* stands in sharp contrast to *F. vesiculosus*. Each dichotomy shows a different growth potential between the two arms, but the amount of difference decreases from the base of the plant upwards. If the lower dichotomies on a plant are examined it will be found that

one arm has produced a good deal of frondage but that the other has done very little. It forks only rarely and its growth-rate is extremely slow. In Fig. 11 only very little frondage has been produced by one arm of the second and third dichotomies. Following the dichotomies upwards it can be seen that there is an acropetal gradient of increasing activity, although the difference in potential between the two arms is maintained. In other words the basal part of the plant has a high degree of latency compared with the distal frondage.

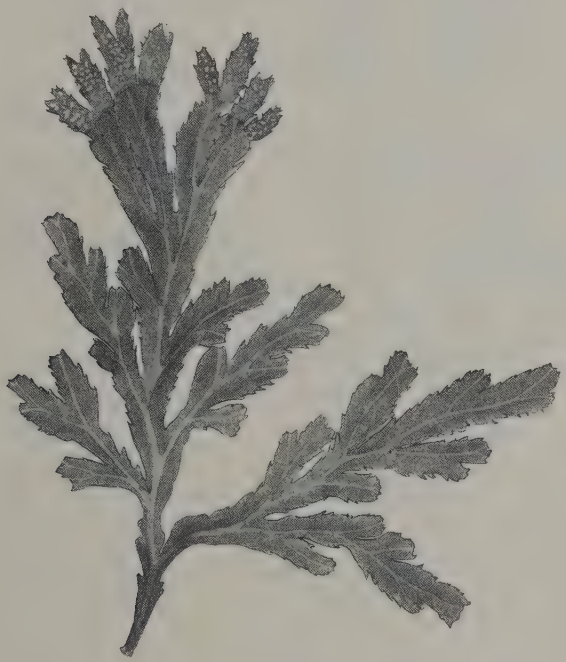

Fig. 8. First year plant of *Fucus serratus* showing unequal dichotomy. ×0·27.

When reproduction sets in, it affects the distal frondage of both arms of the youngest dichotomies and there is no prominent vegetative leader as in *F. vesiculosus*. This is clearly to be seen in Fig. 11 where receptacles occupy distal positions. When the reproductive frondage is excised, further extension of the frond must take place by the activity of vegetative apices lying below the perimeter of the plant. Vegetative apices lie at all levels on the plant and are of various ages. It is the youngest of these tips nearest to the periphery which first begin to accelerate while the peripheral fruiting fronds are degenerating. After successive fruitings, apices lying at successively lower levels take up the role of elongation, and last of all, if the plant survives long enough, the vegetative apices at the base of the plant.

In the first year of growth reproduction may not affect all the peripheral tips. Some may remain vegetative, with the result that elongation is a continuous process, but after the second year, when peripheral tips become reproductive, elongation of the plant takes place by a kind of relay system.

The habit of retaining vegetative frondage on the lower parts of the plant gives *F. serratus* a much more bushy form than *F. vesiculosus*. Bearing in mind

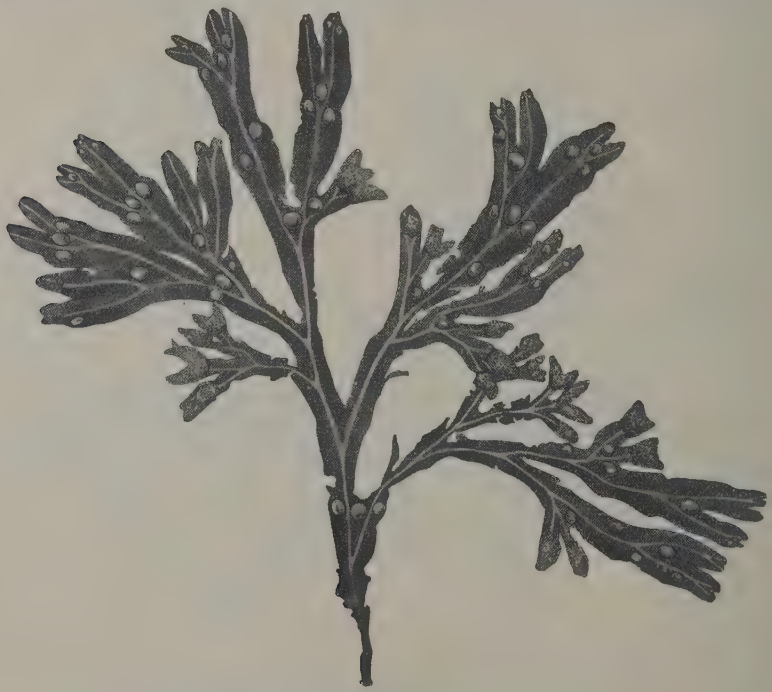

Fig. 9. Eighteen months old plant of *Fucus vesiculosus* showing unequal dichotomy. ×0·21.

that the behaviour of the main fronds is repeated in the secondary branches it will be realized that the body of an old plant of *F. serratus* is built up on a complicated system of branching.

Comparison between the habit of branching in *F. serratus* and the sympodial habit of branching of higher plants is inescapable. The similarities which exist between the mechanisms whereby plant form is achieved by plants on land and plants in the sea is striking.

Plants of both species normally live 3 years (Rees, 1932) and some may survive a fourth and even a fifth year in very sheltered positions. Plants in the

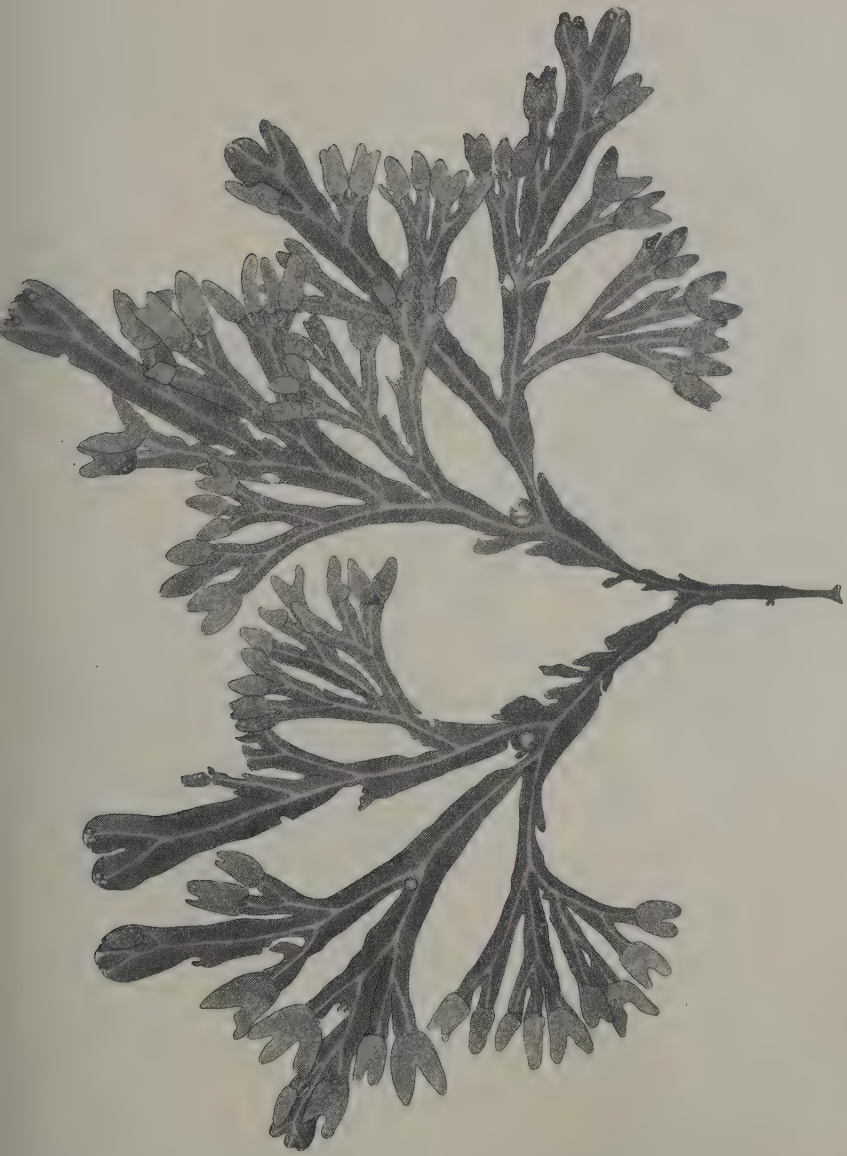

Fig. 10. Plant of *Fucus vesiculosus* with vegetative leaders extending in preparation for next season's frondage-development. ×0·29.

most exposed situations rarely live longer than 2 years. *F. vesiculosus* plants in moderately exposed situations achieve their maximum weight in the fruiting season of their third year, but plants of *F. serratus* may gain in weight in their fourth year and are commonly heavier than *F. vesiculosus* on account of their more bushy habit. In both species the weight of the fronds at the end of the

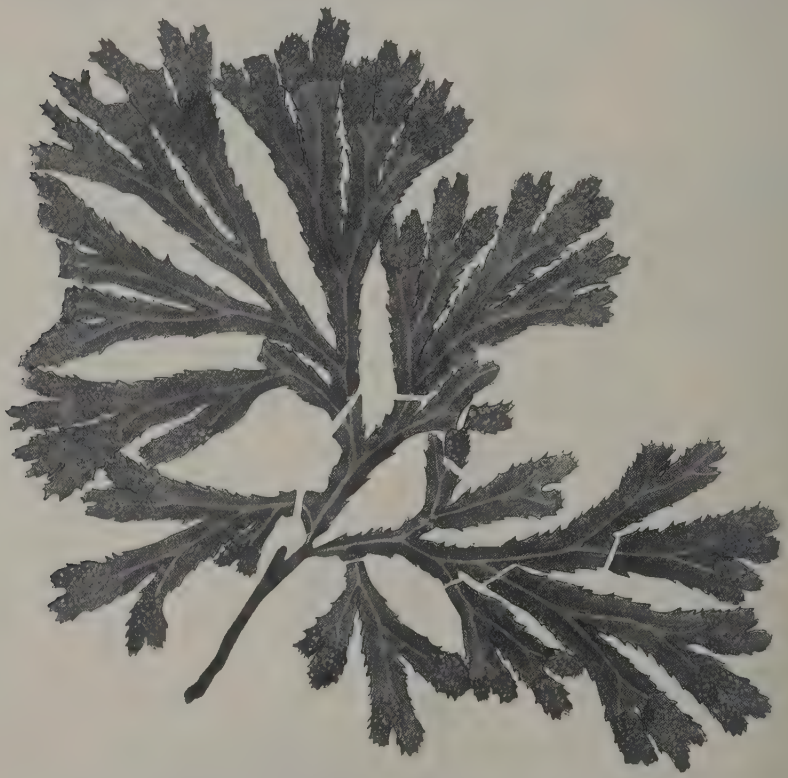

Fig. 11. *Fucus serratus* plant illustrating the amount of defoliation that occurs after fruiting. Fronds distal to the gaps will be shed. ×0·27.

first year is from 1 to 2 oz. (28 to 57 g.); weight increases to about 1 lb. (454 g.) in the second year, and rises steeply in the third year to several pounds. The greatest weight recorded for *F. serratus* was 6½ lb. (2·95 kg.). This is an exceptional weight and was recorded for a plant in its fourth year, growing in a sheltered situation.

Frond-width shows some variation. Cotton (1912) suggests that breadth increases with shelter. To a large extent this suggestion has been confirmed

by observation in the course of the present investigation. It is true that plants of *F. vesiculosus* in extremely exposed places show narrow, dark-coloured and tough fronds. Apart from this generalization, however, there is a great deal of variation in frond-width shown by plants growing even in sheltered situations. Such variation is often accompanied by diversity in number and shape of vesicles and receptacles, and is to be regarded as attributable to factors other than exposure. Broad thalli are commonly found on very young plants, especially where they develop on cleared ground, but frond-width on these young plants may be reduced with each successive addition of frondage. When denudation of the wings of the lower part of the thallus takes place, there may be eventually no sign of the original broad frondage.

Vesicle-formation in *Fucus vesiculosus*

Vesicles are formed in spring. Appearing in March, the vesicles increase in numbers during April, being added serially by activity of apical tissue (Fig. 12). The great majority of them have been laid down by the end of April, but occasional vesicles may be added in June and July and even as late as August.

The vesicles first appear as minute globular swellings in the wings of the frond, immediately behind the apical notch (Figs. 12, 13). They usually arise in pairs, but a single one is often formed also in the angle formed by a dichotomy. They may occur in the lower internodes of large receptacular fronds.

Plants form vesicles when they have reached a length of from 10 to 14 cm. Young plants which have not reached this length by the end of the vesicle-formation period postpone the process until the appropriate time in the following year. It is clear that the seasonal process of vesicle-formation—a process lasting for a few weeks only—must be brought about by seasonal changes in the physical factors of the environment, but there must also be an internal control which permits of vesiculation in plants at a certain stage of maturity and prevents it in plants below the limit of size.

Speaking generally, vesiculation appears to bear some relation to vertical distribution. This is most marked in the upper limits of the zone, for plants found high on the shore where they are mixed with *F. spiralis* frequently show few vesicles or even none at all. These forms have been considered by some authorities (Cotton, 1912) to be a distinct variety, *F. vesiculosus* L. var. *evesiculosus* Cotton. On the coast of Argyll, however, on the Serratus Rock station a high belt of *F. vesiculosus* growing above the *Ascophyllum* zone bore a conspicuous number of vesicles. An almost complete absence of vesicles characterizes the whole *F. vesiculosus* zone, on the Devon, Manx and Argyll coasts, in very exposed places such as the foot of vertical cliffs exposed to full surf-action. There is a possibility that this condition depends on degree of exposure.

From the point of view of vesiculation, the species shows so much variety that it is difficult to describe what might be considered the normal condition.

Vesicles may be in pairs with one axillary vesicle, or the latter may be absent. The numbers of pairs in the internodes may vary from one to ten or more. Usually the vesicles are grouped near the sixth internode on young plants and affect one to four of the internodes of each yearly addition of frondage; but there are plants, attributed to a distinct variety, *F. vesiculosus* L. var. *vadorum* Aresch. (Fig. 14), in which vesiculation appears to be a continuous process. As many as ten pairs of vesicles may occur in the length of one internode, and there appears to be no recognizable gap between the sets laid down in

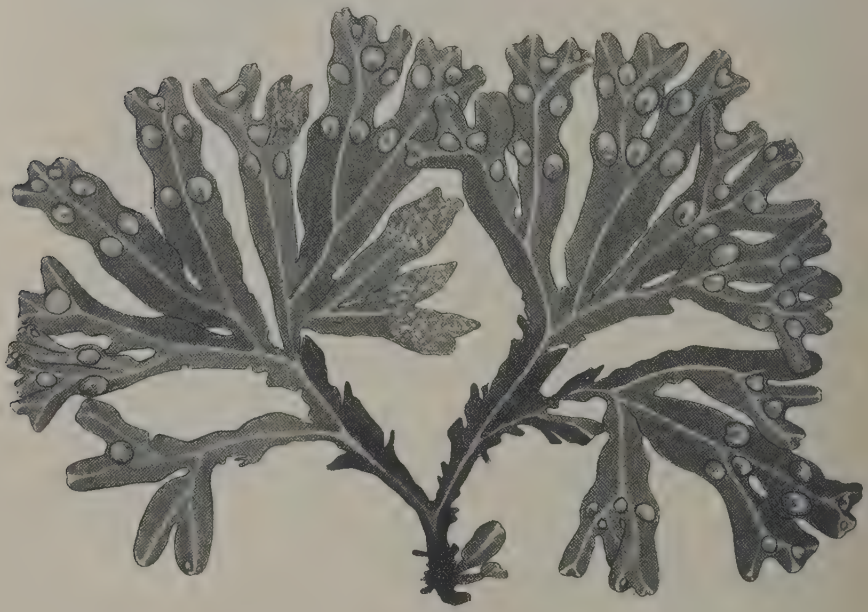

Fig. 12. Vesicle-formation in a plant of *Fucus vesiculosus* L. in the spring. ×0·40.

successive years. This form is frequently associated with a sheltered habitat, but there is evidence that it occurs also in less sheltered places. It has been suggested that vesiculation increases in less well-aerated waters, but this hypothesis has yet to be proved.

Fig. 13 might be considered as illustrative of the most usual arrangement of vesicles, with one to three pairs in the internode and one axillary vesicle, and with a distinct gap between one set of vesicles and the next. The first vegetative period in the plant's life is marked by the production of the first set of vesicles and the frondage between the two sets of vesicles has been developed in the second year.

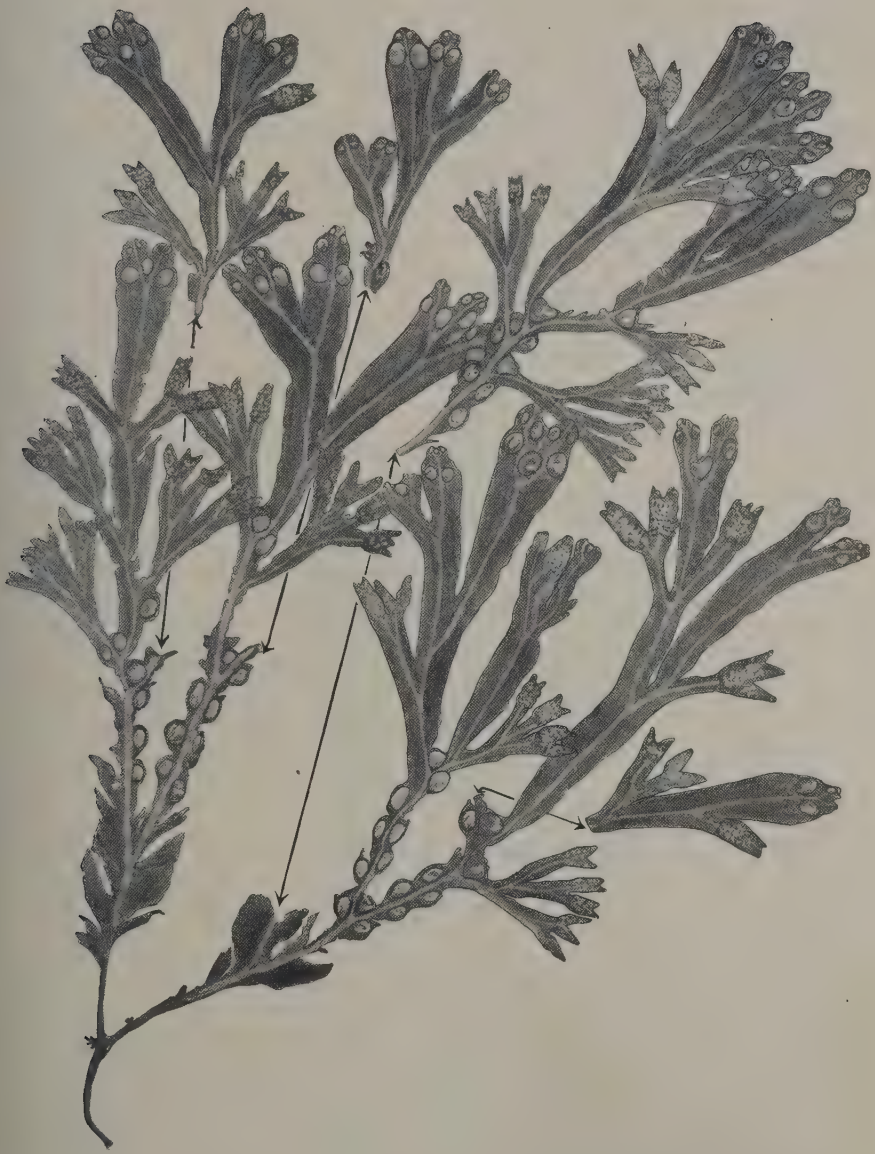

Fig. 13. Plant of *Fucus vesiculosus* L. with first and second set of vesicles. ×0·23.

The number of sets of vesicles present on a plant may thus be used as a criterion of age. This criterion, however, breaks down in an old plant, if the lowest set of vesicles has been removed by denudation of the wings of the basal part of the frond. Distribution and number of the vesicles is the character which most greatly affects the general appearance of the plant. Many of the varieties claimed by various authors are distinguished from one another largely by their characteristic number and arrangement of the vesicles.

Fig. 14. *Fucus vesiculosus* L. var. *vadorum* Aresch. ×0·32.

Figs. 14–19 will illustrate the range of form-variation met with in the course of the investigation. It is difficult to determine without far-reaching genetic and cytological inquiry whether these forms are fixed varieties or not. They have been accepted as such by many algologists (Gard, 1916). In some of the forms illustrated there is close agreement with the descriptions of accepted varieties, but the authors have not had opportunity to consult type specimens. Fig. 15 with a single vesicle in the axils of forks and a very wide divergence of

the arms agrees with the description of *F. vesiculosus* L. var. *divaricatus* Good. & Woodw. Similarly, Fig. 14 may be a young plant of *F. vesiculosus* L. var. *vadorum* Aresch., in larger plants of which there may be as many as ten pairs of vesicles per internode. It is possible that Fig. 16 represents a hybrid between *F. vesiculosus* and *F. serratus*. Such hybrids between the two species are not uncommon; they usually have the vegetative features of *F. vesiculosus* and a receptacle-form more nearly resembling that of *F. serratus*. Fig. 17 represents an unidentified variety which was quite distinct from the evesiculate type characteristic of high levels or exposed coasts. Fig. 18

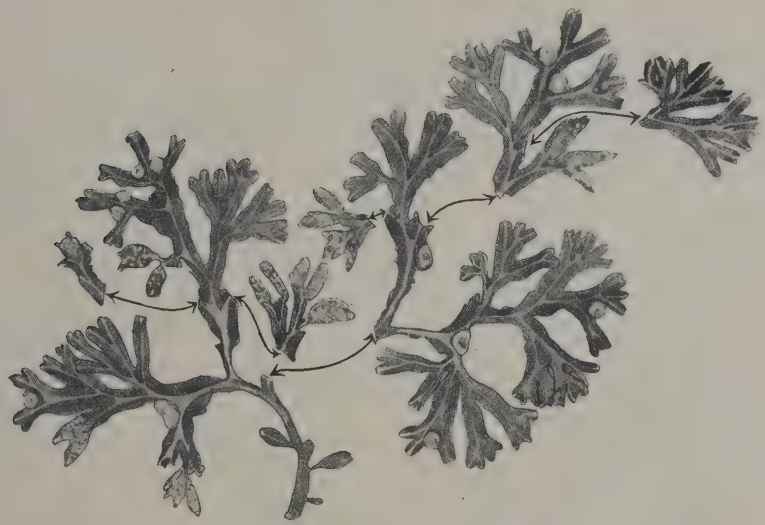

Fig. 15. *Fucus vesiculosus* L. var. *divaricatus* Good. & Woodw. ×0·31.

shows a plant almost without vesiculation but bearing small spherical, air-filled receptacles agreeing in form with the description of *F. vesiculosus* L. var. *sphaerocarpus* J. Ag.

The presence of fresh water draining down the shore affects the form of plants of *F. vesiculosus* lying in its path. On these plants receptacles are usually greatly distended and water-filled (Fig. 19). The same general character is shown by the *F. vesiculosus* population of the banks of the river Mersey, where the salinity of the water is less than that of the open sea.

It is quite certain that the varieties met with are not all to be explained on the score of ecological growth-forms, due to differences in habitat. It is true that modification in vesiculation in relation to bathymetric level is an observed fact; but such modification is defined in terms of growth-rate and internode length as well as in the presence or absence of vesicles; moreover, the range of

variation shown in relation to level is much less than that shown by the different habit-forms described for plants growing side by side at the same level in what appear to be identical circumstances. The extreme forms are linked by a series of intergrades. If they are not to be regarded as fixed, separate varieties, the only explanation of their occurrence would be that *F. vesiculosus* is subject to spontaneous form-variation unrelated to the physical factors of the environment.

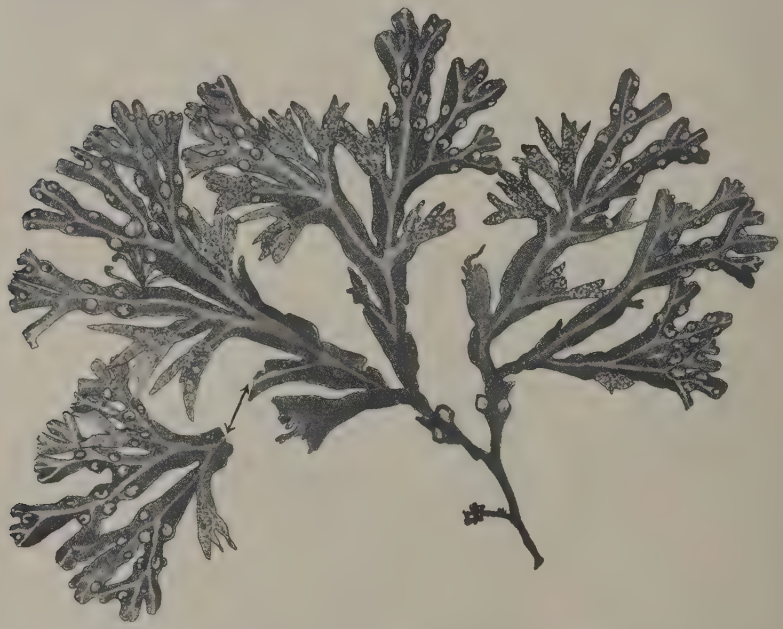

Fig. 16. Suspected hybrid of *Fucus serratus* L. and *Fucus vesiculosus* L. ×0·27.

Reproduction

Reproduction shows a seasonal rhythm. Initiation, maturation of receptacles and retrogressive stages after gamete-release cover a long period. The peak of reproduction is reached in the spring and summer by *F. vesiculosus*, and in the autumn and winter by *F. serratus*, though the latter species shows great variety in the timing of reproduction at various points on the British coasts.

Initiation of receptacles is continued over a period of at least 5 months, and 3 months are required for the development of a receptacle from its initiation up to the stage when gametes are released.

Receptacle-initiation begins in a few plants at first and only gradually affects the bulk of the population. When the peak of gamete-release is passed, some plants continue the process for some weeks. In general, plants in the upper levels begin to fruit first and plants at lower levels come successively into fruit. The timing of receptacle-formation also appears to be affected by the degree of shelter. In sheltered localities reproduction may be initiated earlier than in

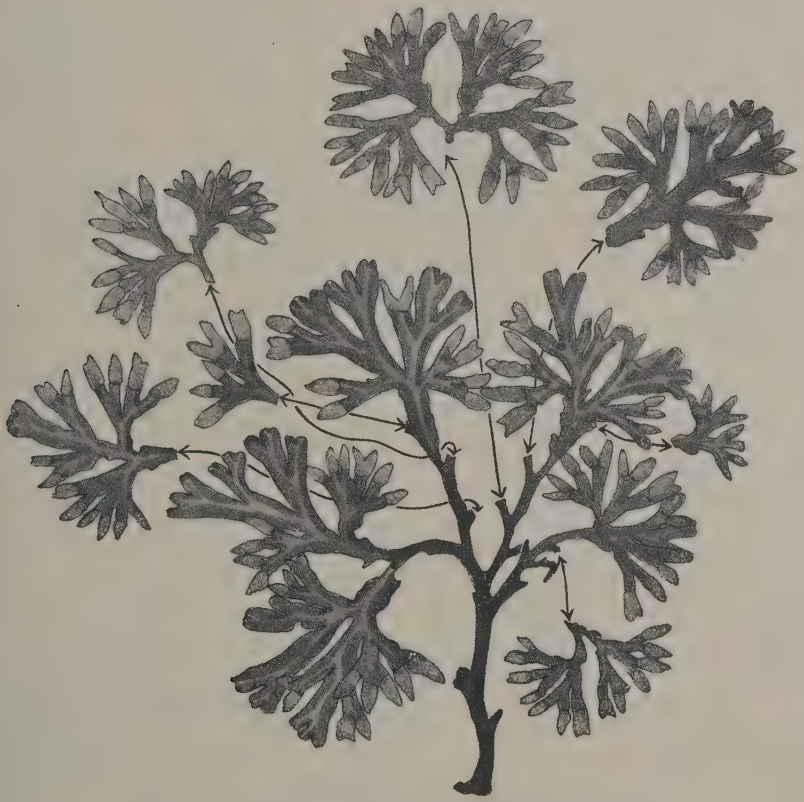

Fig. 17. Unidentified variety of *Fucus vesiculosus* L. ×0·34.

exposed places, and the reproductive stages may be passed through more slowly, thus prolonging the whole reproductive period.

After initiation of new receptacles is over for the season, those still present on the plant pursue the later stages of retrogression, and some of them may be still present on the plant when the next season's receptacles are beginning to be formed.

Young plants of *F. vesiculosus* usually reach a length of 15–20 cm. before they form receptacles. The corresponding length for plants of *F. serratus* is 18–25 cm. Only a small proportion of the plants fruit in their first year. On these plants receptacles are few and are developed on the lowest frond branches. Not infrequently, the frondage produced in the first year becomes reproductive simultaneously with the frondage of the second year. First year plants may

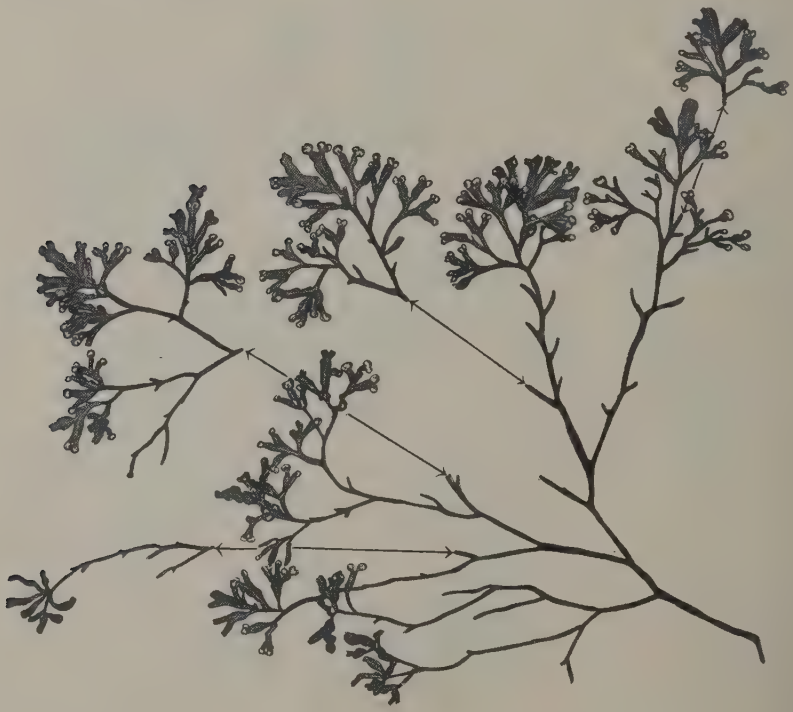

Fig. 18. *Fucus vesiculosus* L. var. *sphaerocarpus* J. Ag. ×0·20.

reproduce either early in the season before the older plants (Port Erin) or later in the reproductive season after the older plants have fruited (Devon).

The receptacles of *F. vesiculosus* and *F. serratus* differ somewhat in development. The apical cell, giving rise to a receptacle in *F. vesiculosus*, continues activity until the receptacle is shaped, but ceases to divide before the oogonia and antheridia are established in the conceptacles. The apical groove then flattens out, and further elongation and swelling of the receptacle is brought

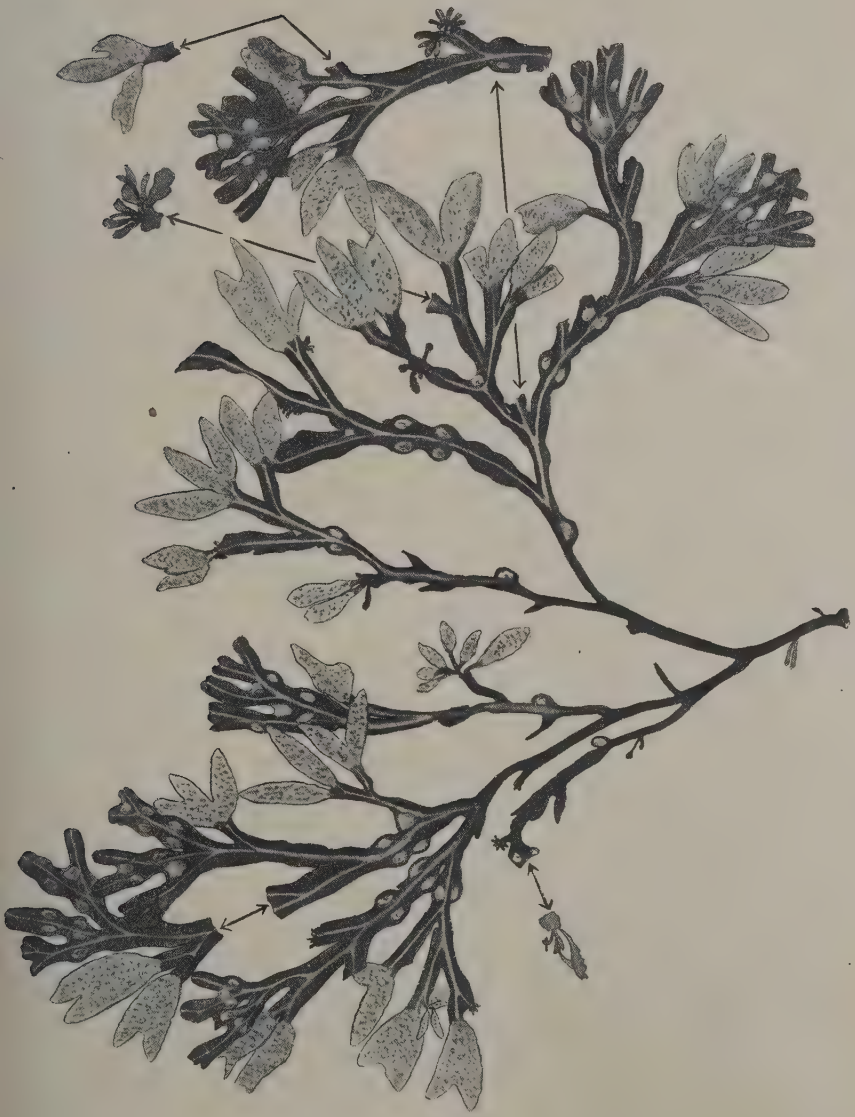

Fig. 19. Plant of *Fucus vesiculosus* L. showing the influence of fresh water. ×0·25.

about by secondary extension of tissues and by increase in swelling of the mucilage of the cell walls. The apex may dichotomize once or twice before it ceases to function. In *F. serratus* the apical cell retains its activity for a much longer period and may be responsible for several dichotomies before it dies out. The receptacles of *F. serratus* may achieve considerable length; they often reach a length of 14 cm.

Occasionally the apices of receptacles in *F. vesiculosus* show variation by retaining their power of cell-division for a much longer period than is normal. The tissue behind the apex forms a very long receptacle with a series of conceptacles interrupted by one or more sterile bands. This peculiarity is usually shown by receptacles developing out of the normal fruiting season.

Though the formation and ripening of the receptacles is a continuous process, it has been arbitrarily divided into serial stages for purposes of making comparative records in the field. The stages are as follows:

(1) Receptacles just indicated by swelling and thickening of the extreme tips of the fronds.

(2) Receptacles swollen and shaped, but with no conceptacles visible to the naked eye.

(3) Conceptacles initiated and their positions just discernible when the receptacle is held up against the light.

(4) Conceptacles shown as faint dots against the light.

(5) Conceptacles showing clearly as *dark* dots against the light; gametes forming but not yet ready for release.

(6) Free release of gametes.

(7) Base of the receptacle emptied.

(8) Receptacles completely depleted and beginning to decay.

(9) Receptacles worn off and their positions indicated by the torn edges of subtending frondage and, later still, by mere spines of midrib from which the wings have been removed.

All three areas showed agreement in the sequence of stages in reproduction, but the periods of the year at which the stages were shown were not coincident.

Reproduction in Fucus serratus

From the many records of fruiting of *F. serratus* on the Devon coast, a typical example may be selected. In February 1942, six groups of young plants, varying in length from 17·5 to 48 cm., were labelled and observed at frequent intervals until August 1944, covering a period of 2 years and 6 months. Two complete reproductive cycles were thus included in the experimental period.

Apart from slight individual variations the groups behaved similarly. The course of reproduction is illustrated by Fig. 20, and details are given in

the following schedule. The timing of reproductive stages in *F. serratus* in the Isle of Man is given for comparison:

Comparison of the timing of stages of reproduction of Fucus serratus *on the Devon and Manx coasts*

	Wembury, Devon		Port Erin, Isle of Man
Apr.	Thickening observable in tips of fronds of largest plants.	Aug.	A few frond tips show thickening.
May	Initiation of receptacles general in population.	Sept.	Initiation of receptacles general in population.
June	Initiation of new receptacles still continues. Those formed earliest have reached the stage of forming oogonia and antheridia.		
July	There is still some initiation of new receptacles. The first gametes are released at the end of the month from the older receptacles.	Oct.	Initiation of new receptacles still continues at reduced rate. The majority of receptacles are approaching maturity and a few have reached the stage of gamete-release.
Aug.	Initiation of new receptacles wanes and release of gametes is general.	Nov.	No further initiation of receptacles takes place and gamete-release is general in the population.
Sept.	No further receptacles are initiated and gamete-release continues. Depleted receptacles show deterioration stages.	Dec. Jan.	Gamete-release begins to wane and all stages in deterioration of depleted receptacles are to be found.
Oct. Nov. Dec.	Receptacles formed late in the season may be still releasing gametes, but deterioration of the majority of the receptacles reaches the last stages.	Feb.	Very few receptacles still release gametes. Most of them are torn off and the plants present a battered appearance.
Jan. Feb. Mar.	Sterile period, though a few old depleted receptacles may be found on the plants.	Mar. to July	Sterile period in which old empty receptacles are rare.

On the more sheltered parts of the Manx coast, at Castletown and Port St Mary, receptacle-formation begins in July, nearly a month earlier than on the more exposed Port Erin beach. The peak of gamete-release is also reached a month earlier, but the whole fruiting period is longer than that for plants on exposed beaches, so that the end of the fruiting periods for plants in both habitats coincides.

The fruiting period for *F. serratus* on the Argyll coast begins 3 weeks later than on the Devon coast, and is therefore intermediate in time between that station and the sheltered coasts of the Isle of Man.

Apart from observations made at the three stations under discussion, there is evidence that the range of times of fruiting of *F. serratus* may be considerably extended elsewhere. Plants of *F. serratus* in full release of gametes have been observed on the Northumbrian coast in July, a date earlier than for any other station.

The degree of fruiting, i.e. the number of receptacles per plant and the proportion of plants in fruit simultaneously in the population, varies from one station to another. From the records, it appears to be heaviest in exposed places. At Port Erin in December, just after the peak of gamete-release, the average percentage of the population bearing receptacles was 60. On a strip running right through the *F. serratus* zone the proportion of fruiting plants varied from 40 to 70 %, being heaviest in the lowest third of the strip. The records from Wembury do not show so high a proportion of plants in fruit. The discrepancy may be due to the fact that a much larger proportion of young plants fruit in their first year on the Manx than on the Devon coast.

Comparison of the proportions of fruiting to sterile tips per plant on the two stations shows a much higher percentage of receptacles on the Manx plants.

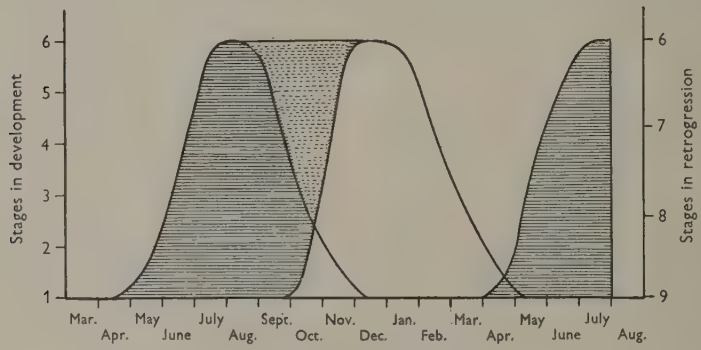

Fig. 20. Seasonal fruiting in *Fucus serratus* on the Devon coast.
See p. 474 for definition of stages.

In many 3-year-old plants, only 5 % of the tips remain sterile; individuals have been found also in which every apex has been transformed into a receptacle (Fig. 26, p. 485). Fig. 21 shows a typical young plant from Port Erin, fruiting for the first time when it was only 10 months old. Fig. 2 (p. 454) illustrates a plant from the Devon coast which has not yet fruited though it is 1 year and 2 months old. Fig. 22 shows a plant of *F. serratus* from Wembury fruiting for the first time in its second year; the receptacles on the plant represent 58·7 % of the total frond-tips.

Reproduction in Fucus vesiculosus

The series of stages in the reproduction of *F. vesiculosus* and the length of time required for their development correspond with similar data for *F. serratus*, but the timing of reproduction is different for the two species.

A comparison of the timing of equivalent stages in reproduction of *F. vesiculosus* on the Devon and Manx coasts follows:

Comparison of timing of stages of reproduction in Fucus vesiculosus *on the Devon and Manx coasts*

	Wembury, Devon	Port Erin, Isle of Man
Dec.	Earliest stages in receptacle formation observable in some of the plant population.	Earliest stages of initiation shown by plants of less than 1 year old.
Jan.	Initiation of receptacles general in the population.	General initiation of receptacles on plants of all ages.
Feb.	Older receptacles swollen and shaped. Initiation of new receptacles is continued.	New receptacles still being formed. The older ones show the positions of conceptacles.
Mar.	A few new receptacles may be formed but the majority have advanced to the stage when conceptacles are just discernible.	No further initiation of receptacles, but those already formed may have reached the stage of gamete-formation. Release of gametes begins.
Apr.	No further initiation of receptacles. Antheridia and oogonia formed in older receptacles.	Release of gametes increases towards the end of the month.
May	Full release of gametes.	Gamete-release passes its peak and the older receptacles show all stages in deterioration.
June	Many receptacles show deterioration stages and the youngest are releasing gametes.	
July	Release of gametes comes to an end and receptacles show all stages of disintegration.	10 % of the population may still be releasing gametes and the rest bear depleted receptacles.
Aug.	Only depleted and decayed receptacles present.	Plants releasing gametes fall to 3 % of the population. Receptacles in the rest of the population are fast disappearing.
Sept.	Sterile period.	Fruiting finished. Initiation of new receptacular fronds.
Oct.		
Nov.	A few tips may show the earliest stages of receptacle-initiation.	

There is only about 1 month's difference in the timing of reproduction on the Manx and Devon coasts. The Devon plants begin first (Fig. 23 and Table XXXIII, facing p. 514). Another point of difference lies in the reproduction of young plants. On the Devon coast they usually bear receptacles late in the season, after the main population is in fruit. On the Manx coast, the fruiting of young plants usually precedes that of the older plants. There is also, as was described for *F. serratus*, a precocity of fruiting shown by plants in sheltered situations. On the promontory of Langness on the south-east coast of the Isle of Man, where there is considerable shelter, the factors of the environment combine to make the locality particularly favourable to algal development. Not only do young plants grow more quickly in this area, but they come into fruit at least 3 weeks earlier than on any other area. This precocity is hard to explain unless it be that a river about a mile away may contribute extra organic

nutrient matter to the sea water in the neighbourhood. The set of the tides is such that mud in very small quantities is carried by the tide and deposited above the algal zone. The mud is just sufficient to support a very narrow belt of saltmarsh.

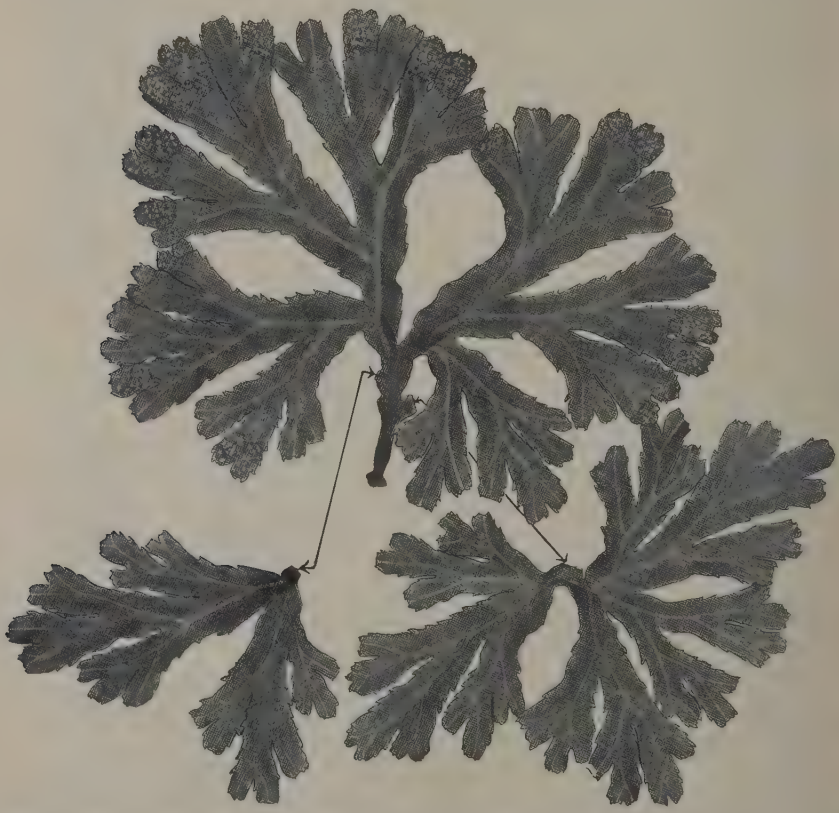

Fig. 21. Plant of *Fucus serratus* from the Manx coast showing distal fruiting in the first year. × 0·29.

With *F. vesiculosus* as with *F. serratus* a higher proportion of young plants fruit within the first year on this coast than on the Devon coast. Clearance was effected, in the first week of August, of a strip running through the *F. vesiculosus* zone. Analysis of the new population 37 weeks later showed that 70 % of young plants over 14 cm. in length bore receptacles. The fruiting branches bore only one or two receptacles. In the second and succeeding years the number of pseudo-lateral fronds destined to bear receptacles increases greatly,

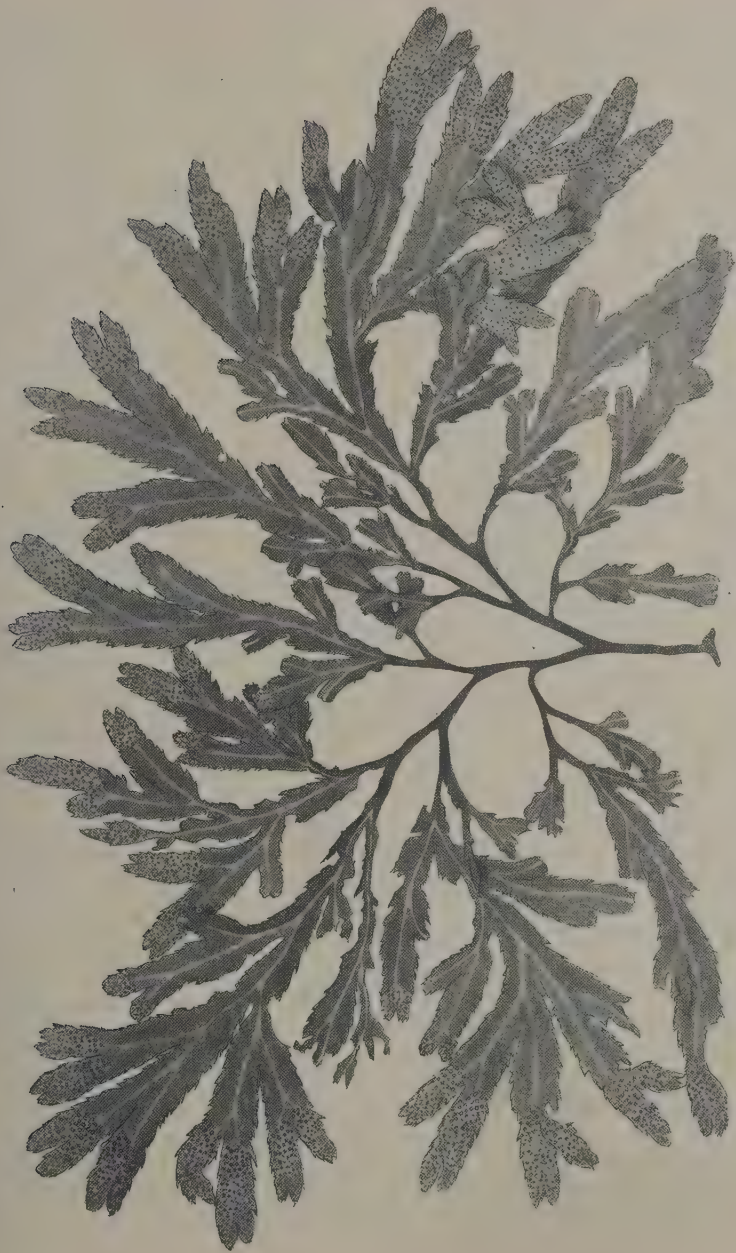

Fig. 22. Plant of *Fucus serratus* from the Devon coast fruiting for the first time in the second year. ×0·29.

thus raising the proportion of fruiting to vegetative tips on the plants. Fig. 24 showing a plant from the Devon coast, illustrates the appearance of plants preparing for reproduction in the second year of growth. Some of the vegetative leaders, by the activity of which next year's frondage will be developed, are projecting, and the shorter, much divided fronds will develop receptacles in the current season.

The proportion of fruiting tips in the third and fourth years may be very high, usually reaching 80–95 % of the total frondage. Some very bushy forms with a relatively low growth-rate may have very few vegetative tips left after fruiting, to carry on development for the following year. Fig. 17 (p. 471) illustrates a plant in which only 18 % of the frond tips remain in a vegetative

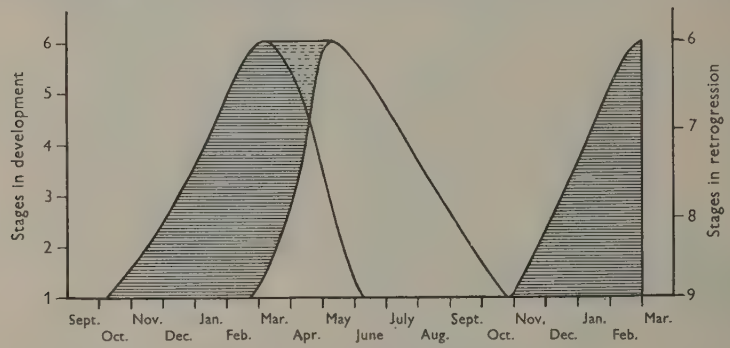

Fig. 23. Seasonal fruiting in *Fucus vesiculosus* on the Devon coast. See p. 474 for definition of stages.

condition. Fig. 25 shows a plant with only six vegetative tips left out of a total of 158.

Except on very exposed localities on the Argyll coast, the time of the fruiting period for *F. vesiculosus* coincides with that for the Devon coast. In exposed places, the plants reach maturity, a month later, at approximately the same time as plants in sheltered localities on the Manx coast.

The sequence of normal phases of behaviour for *F. vesiculosus* on the Manx coast is summarized below:

Jan. The main leaders project beyond the pseudo-lateral fans, which have completed their dichotomies in preparation for receptacle-initiation. Receptacles have been initiated.

Feb. Leaders still undergo extension. New receptacles are still being laid down, but the oldest have reached stage 3. Vesicle-formation may be initiated in a few individuals.

Mar. Most of the new receptacles have been laid down and release of gametes begins from the oldest receptacles (stage 6). Vesicle-formation becomes more marked.

Apr. Vesicle-formation is general. The receptacles are releasing gametes. Initiation of receptacles ceases.

May The peak period of gamete-release is reached and passed. Leaders have now developed pseudo-lateral fans which are in process of dichotomy at short intervals.
June Gamete-release wanes. Old receptacles have reached stage 7. The form of next season's receptacular fronds is discernible.
July Decay of old receptacular fronds takes place. Many turn yellow and are shed.
Aug. Deterioration of old receptacles is nearly complete. New pseudo-laterals have developed into large fans which form the most conspicuous part of the vegetation, and hide the remains of old fruiting fronds.
Sept. A few old receptacles in stage 8 may still be found. New frondage grows in length.
Oct. Final disappearance of old receptacular fronds and further enlargement of new fans.
Nov. Pseudo-lateral frondage prepares for initiation of new receptacles.
Dec. Tips of lateral fronds begin to thicken for receptacle-formation.

The data for this schedule are drawn from the experiments on the Manx station. The schedule would be applicable to the Devon station if the sequence were shifted back about 1 month.

Defoliation

When fruiting is over for the season, both species rid themselves of all frondage which has fruited. The amount of such frondage dependent on the degree of fruiting may be considerable. When the gametes are all shed from a receptacle, it becomes gelatinous and open to the attack of fungi and animal parasites. It is readily rubbed off by friction against the rock, but actual necrosis of tissues also takes place. Necrosis starts in the receptacle but extends to the subtending internodes. The latter are not under control of an apical cell because the apical cell dies out in the later stages of receptacle-formation. Necrosis works basipetally downwards crossing forks if both arms have borne receptacles and is arrested only when it reaches a fork, one arm of which is still provided with a functional apical cell, however distant. In this way all fruiting fronds are shed; all that remains is the axis bearing vegetative apices from which next season's frondage will be developed. Fig. 11 (p. 464) shows a plant of *F. serratus* fruiting for the first time. The gaps in the illustration indicate the frondage which will be shed. New frondage will be produced from vegetative apices while deterioration of receptacular fronds goes on; in the specimen illustrated all new fronds will originate from the half-dozen apices left on the plant. On the Manx coast fruiting in *F. serratus* is heavy, and it sometimes happens that all the apices may produce receptacles. The plant then pays the penalty of 100 % reproduction, being left without a vegetative leader for the production of new frondage (Fig. 26).

The process of defoliation is more gradual in *F. serratus* than in *F. vesiculosus*. In the former species, after reproduction, the frondage shows broken ends and has a very battered appearance for about a month until the upgrowth of new frondage hides the broken ends. The final stages of deterioration are completely hidden under cover of the new frondage which now becomes the most conspicuous feature of the vegetation.

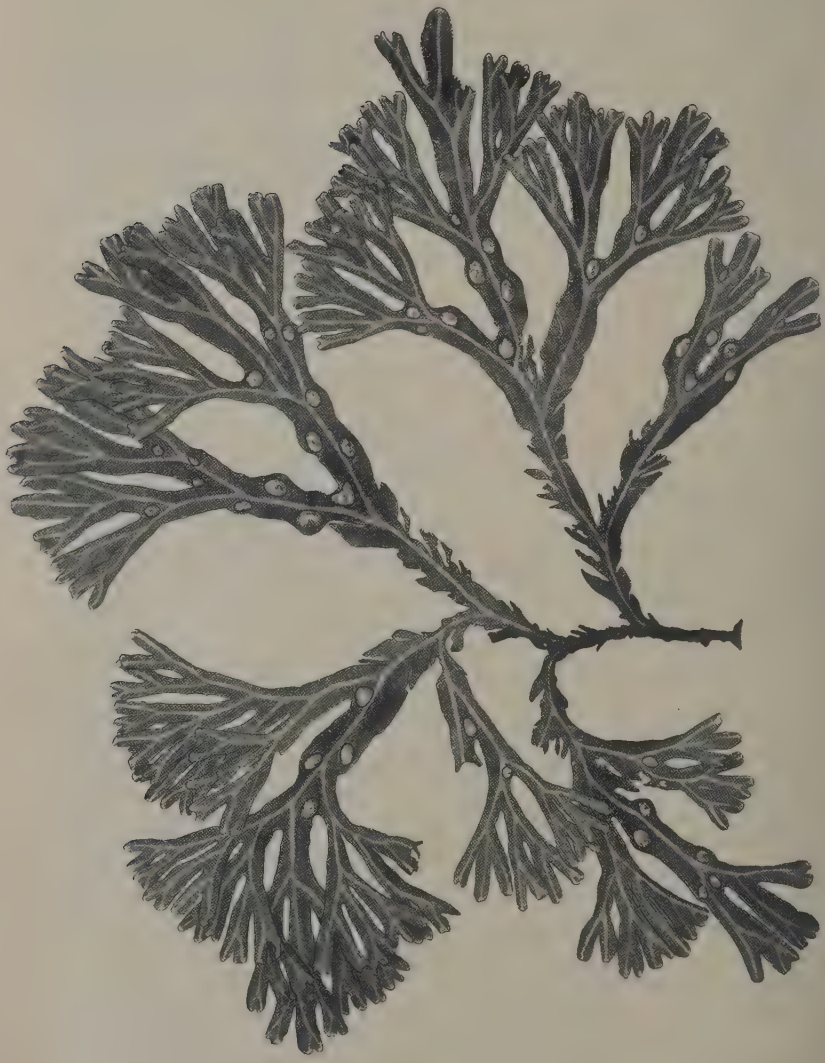

Fig. 24. Plant of *Fucus vesiculosus* from the Devon coast preparing to fruit for the first time in the second year. ×0·275.

In *F. vesiculosus* the pseudo-lateral fronds turn yellow after fruiting. The colour change affects the whole fan simultaneously (Fig. 27); the frond becomes

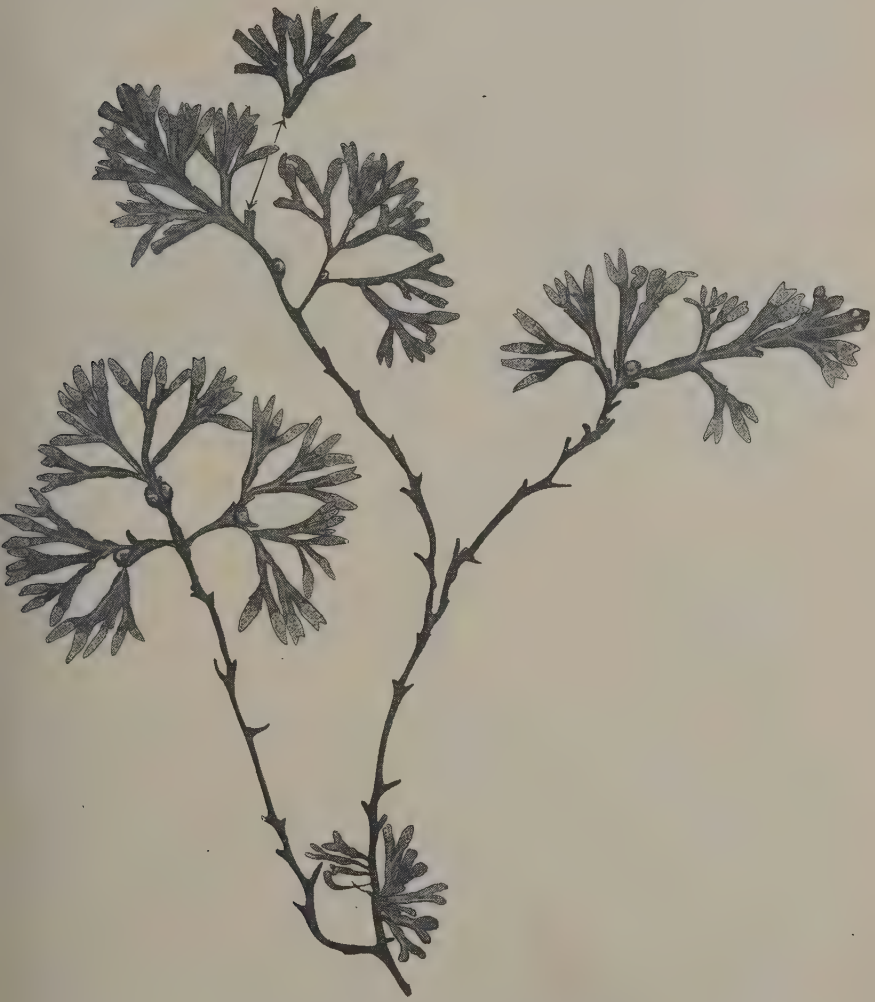

Fig. 25. Plant of *Fucus vesiculosus* with spines' showing the position of excised fronds. Six vegetative leaders only remain. $\times 0{\cdot}23\frac{4}{1}$

limp and gelatinous (Fig. 28) and is ultimately shed more rapidly than that of *F. serratus*. During the deterioration stages the new frondage from terminal leaders and from vegetative apices lower on the plant cover the old

fruiting fans, and the effect of defoliation is not so evident as in *F. serratus*. An old plant of *F. vesiculosus* which has fruited several times usually consists of a tangle of twisted strands from which the wings have been denuded, beset with spines to mark the points of attachment of earlier fruiting fronds and bearing new frondage at the extreme tip of the plant (Fig. 25). The degree of fruiting increases with age and, correspondingly, the loss of frondage increases every year. The evidence of previous fruiting on an old plant is given by the presence of scarcely detectable swellings on the length of the main strands.

Depopulation

Analysis of the populations into age-groups, taken from the experimental areas and from untouched areas alongside, shows a fairly consistent proportion of plants in their first, second and third years, together with a very small proportion of older plants. The analyses of the initial and final populations of *F. vesiculosus* and *F. serratus* on thirty-five 1-metre-square areas at Wembury are given in Figs. 30 (p. 491) and 33 (p. 496).

Table VIII. The Composition of *Fucus* Populations in Year-Classes on the Devon and Manx Coasts

Station	1st year population (%)	2nd year population (%)	3rd year population (%)
Wembury, Devon:			
Normal population	100	57	17·3
Experimental population	100	33·8	5·0
Port Erin, Isle of Man:			
Normal population	100	30·8	10·0
Experimental population	100	31·4	9·5

Mortality is extremely high in the early stages of germination and up to the time when the plants are 3 cm. in length. Much of this loss is undoubtedly due to the depredations of molluscs. That this loss may be severe is shown by experiments carried out on the Manx coast by Orton, Jones and Lodge (Lodge, 1948). Nearly 15,000 limpets were removed from a broad strip running through the fucoid zone on the beach at Port St Mary. The zone was only scantily covered by a sparse fucoid population. After removal of the limpets the zone became covered by a dense growth of *Fucus* which was thick enough to be visible from the air. In the course of 3 years, the limpets have reinvaded the area and the plant population is gradually disappearing. There is now a noticeable scarcity of germlings and the older plants are dying out. A large proportion of the plants reaching the end of their first year are lost during the second year, and only a small proportion survive to the third year. The proportions vary with the physical risks of the environment and depopulation rate rises with exposure. The Devon and Manx areas are compared in Table VIII.

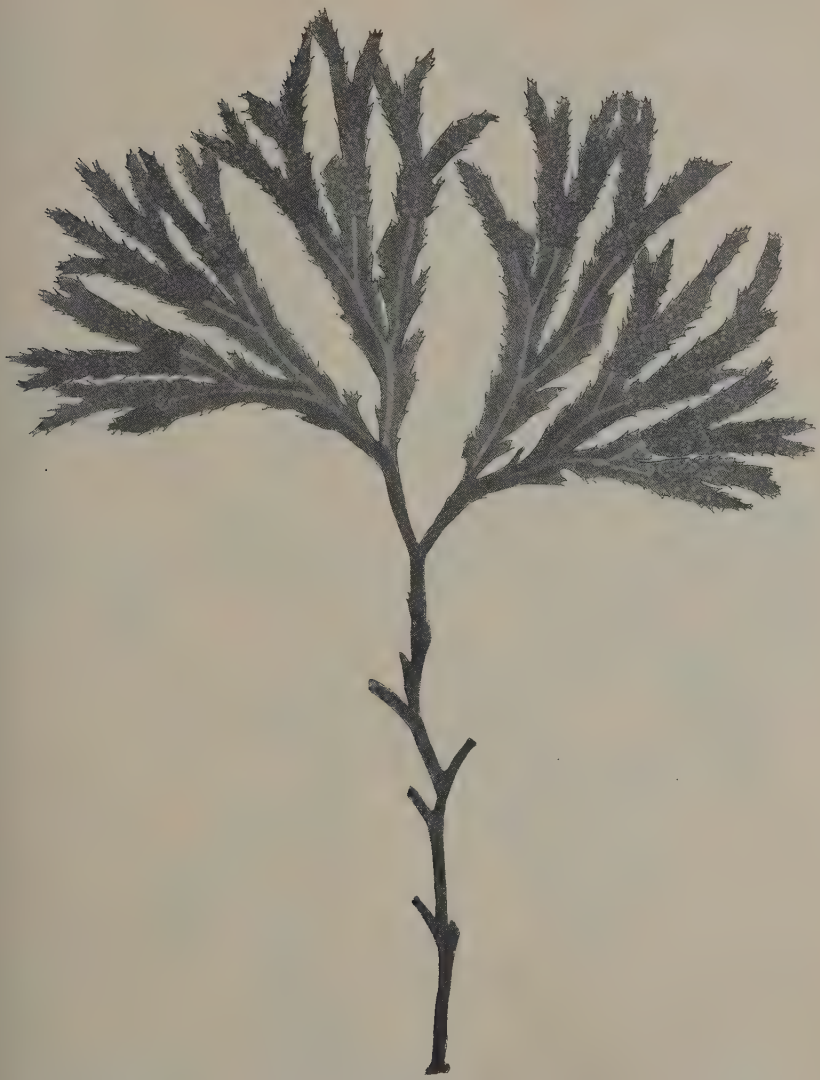

Fig. 26. Plant of *Fucus serratus* in which copious fruiting has left no vegetative apex for further frond-development. ×0·275.

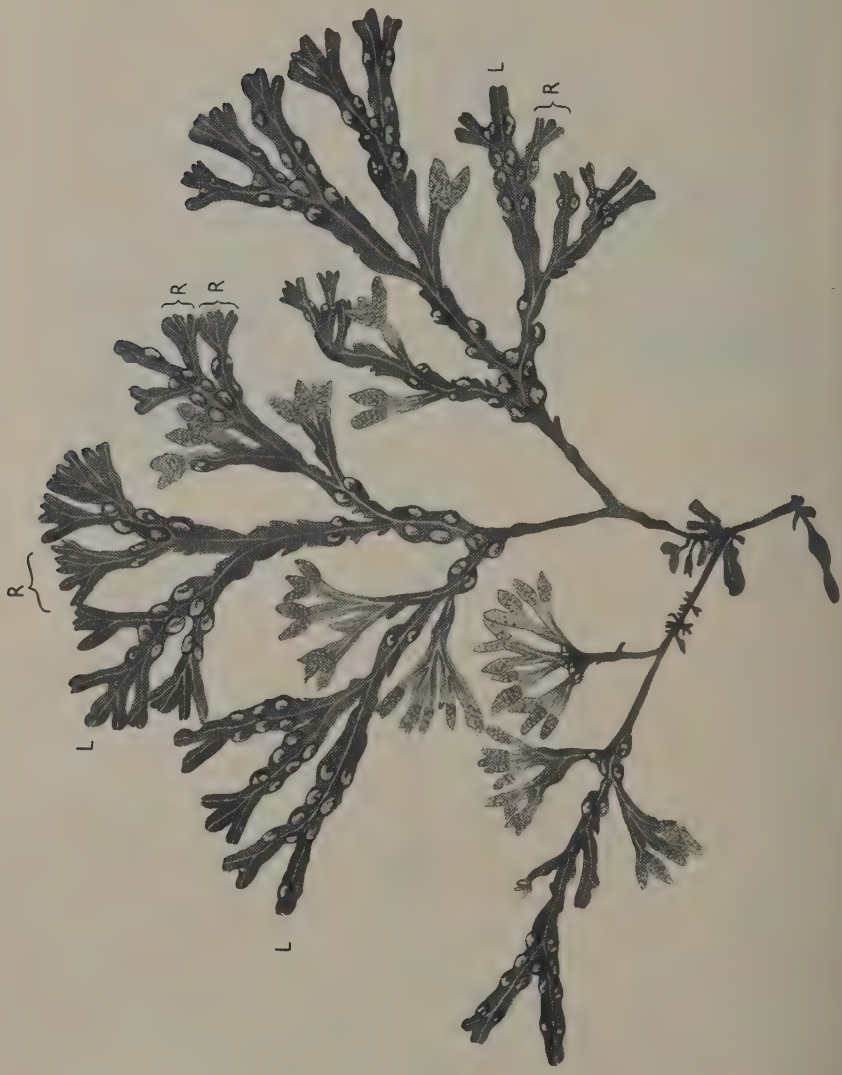

Fig. 27. Defoliation in a plant of *Fucus vesiculosus* from the Manx coast. The fruiting fans turn

In assessing the age-groups in the population, the number of first year plants is taken as 100 %, whatever it may be, and the numbers of plants in the other age-groups taken as percentages of it.

It appears that the experimental and normal populations on the Manx station agree very well. On the Devon coast there is some difference between

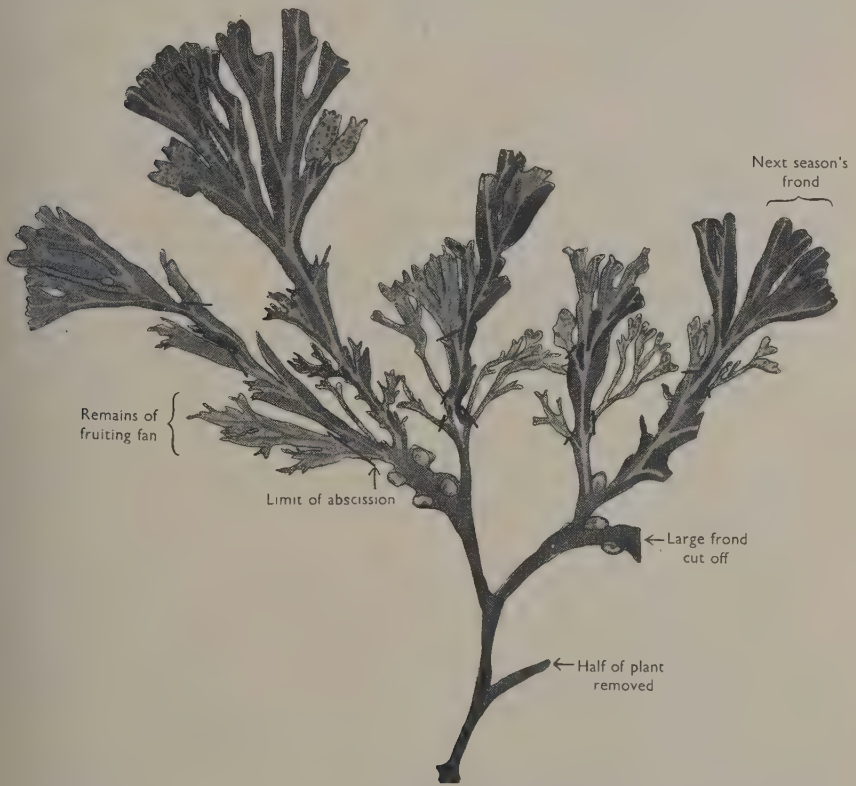

Fig. 28. Plant of *Fucus vesiculosus* showing a late stage in deterioration of the fruiting fans. The limit of abscission is marked by thick lines across the frond. The vegetative leaders are undergoing dichotomies to form next season's fruiting fans. ×0·295.

the two populations. It can be assumed that the fucoid population on the Manx coast, which is exposed, returns to normal after an interval of 3 years from the original clearance, but 4 years would probably be needed before the population returns to normal on the Devon coast.

Repopulation

In order to test the effect of reaping, a series of experiments were undertaken in all three areas. Selected plots either in the form of strips or individual squares at various levels were used for experiment. Some were cleared by scraping the rock with a sharpened putty knife. This did not completely clear the germlings, but was deemed to be equivalent to any method which might be used in commercial reaping. The populations on other squares were cut down to lengths varying from 2·5 to 30·0 cm.

At Wembury metre squares in the *F. serratus* zone were cleared initially at monthly intervals, but were all cleared finally at the same time, with a view to assessing the time required for complete repopulation. The strips at Port Erin were originally cleared simultaneously in order to find the most productive level in the zone. The Scottish experiments consisted in clearing squares at different times and then finally reclearing all at once.

The original and final populations were weighed and analysed to find the numbers of plants in various size groups. The areas selected bore as far as possible pure populations of *F. vesiculosus* and *F. serratus*, but in the strips on areas with great surface irregularity the populations were often mixed. The final populations did not show the same content as the original populations.

Fucus vesiculosus *on cleared areas*

No data for final populations of *F. vesiculosus* are available from the Manx station, but data for this species may be quoted from the Devon and Scottish stations.

On the Devon coast, sixteen 1-metre-square areas were cleared at monthly intervals. The original populations were mainly *F. vesiculosus*, but there was also an admixture of *F. serratus* and *Ascophyllum* (Fig. 29). Five of the squares bore *Ascophyllum* as well as the two species of *Fucus*. In the final populations there was only a negligible amount of *Ascophyllum* and the proportion of *Fucus serratus* was less than in the original populations. Fig. 29 shows a comparison of the weights of original and final populations on the squares. Only one final population showed a pure growth of *F. vesiculosus*. The clearance of the squares in sequence gave opportunity for the settlement of eggs from whichever species was in fruit at the time of clearance, but despite the fact that some of the squares were cleared when *F. serratus* was in fruit and *F. vesiculosus* in the almost sterile condition, the final populations, after a lapse of nearly 3 years, consisted mostly of *F. vesiculosus*.

The total original weight on all the squares was 108·6 kg., and the final weight was 107·1 kg., thus giving a net loss of 1·5 kg. The period of experiment varied for each square, but the interesting fact emerges that, with the exception of square 16, the weights in the final populations exceed those in the original populations on those squares which had the shortest experimental periods.

Square 6 was cleared sixth in the series and was re-cleared later than some of the other squares. It had therefore the longest experimental period of 34 months, yet the final population weighed only 7·4 kg. compared with 9·0 kg. in the

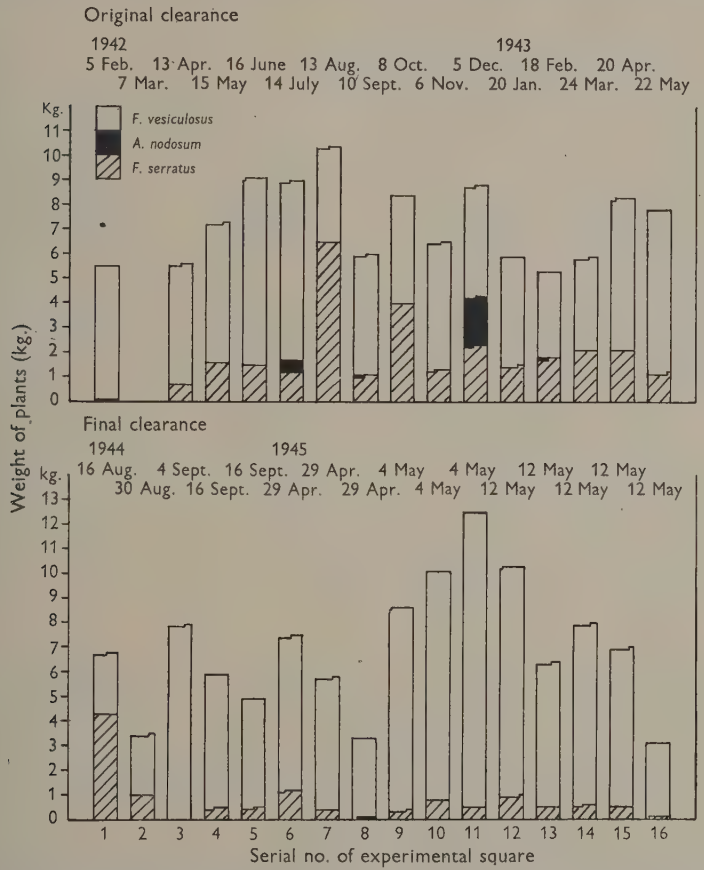
Original clearance
1942
5 Feb. 13 Apr. 16 June 13 Aug. 8 Oct.
7 Mar. 15 May 14 July 10 Sept. 6 Nov.
1943
5 Dec. 18 Feb. 20 Apr.
20 Jan. 24 Mar. 22 May
Kg.
F. vesiculosus
A. nodosum
F. serratus
Final clearance
1944
16 Aug. 4 Sept. 16 Sept. 29 Apr. 4 May
30 Aug. 16 Sept. 29 Apr. 29 Apr. 4 May
1945
4 May 12 May 12 May
12 May 12 May 12 May
kg.
Weight of plants (kg.)
Serial no. of experimental square

Fig. 29. The repopulation of cleared areas by *Fucus vesiculosus* on the Devon coast. Original and final weights of plants on sixteen 1-metre-square areas at Wembury.

original population. Fig. 30 shows an analysis of the plant populations in size groups at the beginning and end of the experiment. Though the total weight of the final populations is slightly less than that of the original populations, the number of plants in the final populations is much greater than in the original populations (Table I, p. 444). In grouping the plants, 27 cm. was taken as the length of a first-year plant, 55 cm. as the length of a plant at

the end of its second year, and over 55 cm. for plants older than 2 years. The lengths were based on growth-rate as determined by experiment. The increase in numbers in the final populations is due largely to the much greater number of young plants.

The time of year at which the squares were cleared does not appear to have had much effect. There was no noticeable delay in the return of germlings to squares cleared between October and March. The squares with the shorter periods cleared in the winter show, in fact, an excess of young plants, partly because the final clearance was made in May, and the young plants then present had obviously developed during the earlier part of the fruiting period of that year.

Plants reach their greatest weight when in full fruit. The fruiting period is a long one, and less difference in the weights was obtained than was expected (Fig. 29). Squares 1–5 were re-cleared in September at the end of the fruiting season when the majority of the plants were sterile; the remaining squares were re-cleared in May, which is well in the fruiting season.

Other final weights of populations developed after clearance on the Devon and Argyll coasts are given in Table XXXII (p. 513).

Since the final population on a cleared square bears no simple relation to the time it has been growing there, other factors must be considered. The conditions which favour settlement of eggs and further development of sporelings may be determined locally by chance factors. The final population may very well depend on variable factors such as weather at the time of settlement of the eggs. Clearing of the square also alters natural conditions and its effects may vary in degree from square to square.

Fucus vesiculosus *on cut areas*

Harvesting of fucoid areas is commonly carried out by cutting the fronds with a bill-hook. New frondage then develops on the cut fronds by proliferation. The power to proliferate is shown much more markedly by *F. vesiculosus* than by *F. serratus*. Sauvageau (1920) refers to the power of proliferation by *F. vesiculosus* on the French coast. Speaking of areas where *Fucus* is regularly harvested, he refers to masses of vegetation produced by proliferation to such a degree as to imperil the attachment of the plant to the substratum. In the present experiments it was found that proliferation took place only from fronds which were provided with an apical cell at the time of breakage, that is, that no proliferation will take place on frondage which had produced receptacles. The size of the proliferation-frondage depends on the age of the cut fronds. Proliferation from young frondage will produce frondage of normal size, but, with increasing age of the cut frondage, the proliferated fronds are more and more stunted and may indeed be extremely minute. Proliferated frondage from an old part of the plant has been noted, which was no longer than 2 cm. and bore minute receptacles less than 0·3 cm. long. It is obvious that in

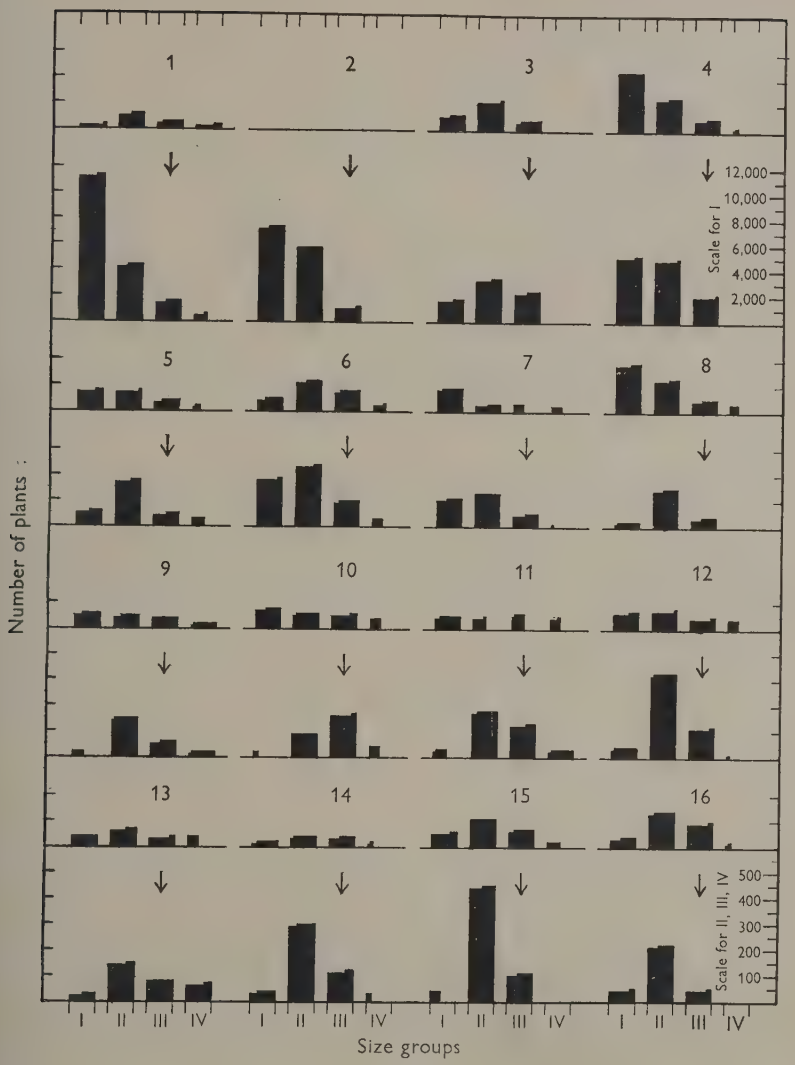

Fig. 30. The repopulation of cleared areas by *Fucus vesiculosus* on the Devon coast. Original and final numbers of plants in size-groups on sixteen 1-metre-square areas at Wembury. Size-groups as follows: I, under 10 cm. in length; II, 10–27 cm.; III, 27–55 cm.; IV, 55 and over. Scale for group I (top right corner) is reduced by a factor of 20.

reaping by cutting, the height of the cut above the base of the plant will have an effect on the amount of new frondage developed by proliferation.

Various experiments were made in which the population was cut down to varying heights above the base of the plants. It was found that, if the level of cutting was at or below 15 cm. from the base, very little proliferation took place, and the cut plants appeared to lose vigour. After the lapse of a year or two, the cut plants disappear under a forest of young germlings. If the level of cutting is 30 cm. above the plant base, proliferation takes place readily and rapidly. The proliferated fronds keep pace with young frondage arising from the germlings which establish themselves between the cut plants. None of the results of experiment on the Devon and Manx coasts showed any parallel with those quoted by Sauvageau. The weed is reaped in France twice a year, in May and in September, and it is held to be more profitable to reap twice than once a year. It does not appear that such a practice would be profitable on the British coasts. Even yearly harvests would give crops consisting of much more frondage from young plants than from frondage arising by proliferation of cut plants.

In an experiment on the Manx coast, 3-metre squares side by side were treated differently. Square A was left untouched, square B was cut to 30 cm. above the base, and square C was cut down to 15 cm. above the base. At the end of 13 months, the populations were weighed. The results were: A, 4·76 kg.; B, 4·11 kg.; C, 2·02 kg. The population of C consisted entirely of young plants and some stumps of the original cut plants which had done nothing in the way of regeneration of frondage.

The results of experiments on regeneration after cutting for *F. vesiculosus* on the Argyll station do not differ greatly from the results of similar experiments on other areas. Data from experiments in the Sgeir Bhuidhe area will serve as illustration.

19 Mar. 1942. Plants on two areas, A and B, were cut down to 8 and 15 cm. respectively.

4 June 1942. No regeneration from cut surfaces had occurred, but there was a little proliferation from the base of the plants and growth from fronds which had been too short to cut.

16 July 1942. Proliferations just beginning on cut surfaces of plants on A and B.

12 Sept. 1942. Considerable devastation of the area had occurred in the interval and many of the plants had disappeared. Proliferations from the base of the plants in B had reached 7·5 cm. in length.

11 Nov. 1942. Very few of the original plants were left and those were denuded of the frond wings. Proliferations from the plant bases had reached 15 cm. in B.

6 Feb. 1943. More deterioration had occurred in the cut population and the stumps were almost hidden under a growth of new plants.

From this point on progressive deterioration followed, and at last there were none of the original cut plants left. It is obvious that no profit would result by

cutting the population at levels less than 30 cm. above ground. In any case the great bulk of the returning population is derived from the upgrowth of new plants.

Fucus serratus *on cleared areas*

A strip, 1 m. wide, running through the entire belt of *F. serratus* was cleared at Port Erin in July 1941. In its upper levels the population of the strip was mixed *F. serratus* (dominant), *Ascophyllum* and *Fucus vesiculosus*. The middle section was pure *F. serratus* and the lower levels ran into the top of the *Laminaria digitata* zone. That part of the strip which carried a pure population of *Fucus serratus* was 9 m. long. The two uppermost squares on the strip were covered by boulders after a storm, but the rest of the strip escaped much interference.

The total weight of the plant population was initially 170 kg., of which 47 kg. was due to *Ascophyllum*. The final weight of the population was 92 kg., representing a total loss in weight of 78 kg. This deficit is in part explained by the fact that *Ascophyllum* did not regenerate itself on the cleared area during the period of the experiment. Sporelings appeared in small numbers and reached a length of a few cm., but inevitably disappeared again. Even at this date, 8 years after the original clearance, there is still no sign of the establishment of an *Ascophyllum* population. There are on an average 20 sporelings of *Ascophyllum* per m^2., the longest of which is only 13·5 cm. Fig. 31 and Table XXXIV (p. 514) show the analyses of the weights and numbers of the final and original populations. A summary of the proportions of the component algae is shown below:

	Original population (kg.)	Final population (kg.)
Total weight	170	92
F. vesiculosus	1	4
F. serratus	87	71
Ascophyllum	47	0
Laminaria	32	17

The *Fucus* population might have been expected to gain advantage by the improvement in lighting of the strip by the removal of the *Ascophyllum*; there is an increase of 3 kg. in the weight of *Fucus vesiculosus* when its competitor *Ascophyllum* was removed and failed to return, but this slight advantage is balanced by the decreased weight of *Fucus serratus* in the final population. There is no permanent population of *Laminaria* at this level on the shore, as the young plants are frequently removed and replaced. Rough weather caused considerable fluctation in the amount of *Laminaria* above L.W.N.T. *L. digitata*, 90 cm. long, was recorded at interim observations, but the long plants had all disappeared when the strip was finally cleared in April 1944. The data from a repopulation experiment from Wembury involving nineteen 1-metre squares, F.S.H. 1–3 and F.S.L. 1–16, may be used to illustrate recolonization on the

Devon coast. Figs. 32 and 33 give a comparison of weights in the original and final populations and analyses of the numbers of plants in various size groups.

A summary of the data is given below:

	Original population (kg.)	Final population (kg.)
Total weight	137·7	133·0
F. serratus	137·4	131·7
F. vesiculosus	0·3	0·5
Laminaria	—	0·8

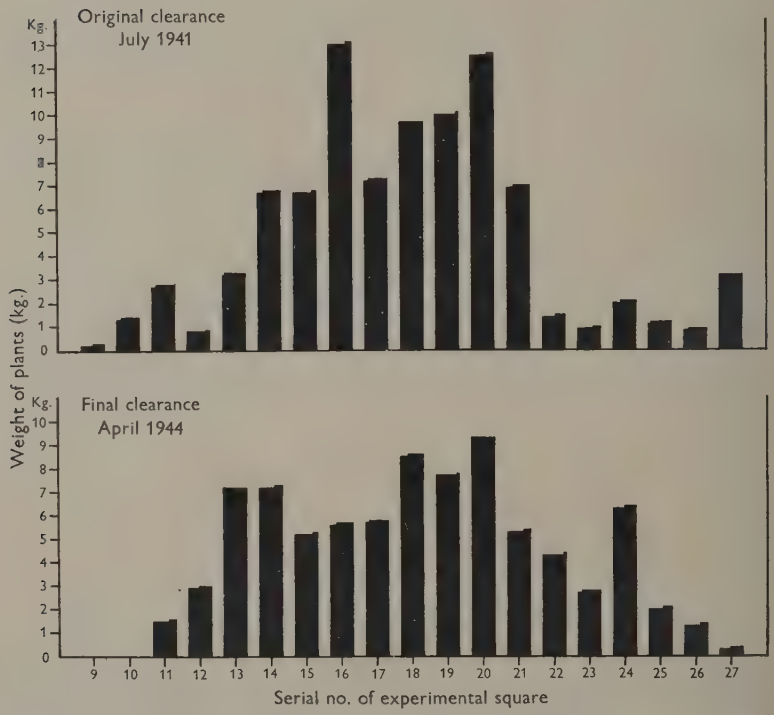

Fig. 31. The repopulation of cleared areas by *Fucus serratus* on the Manx coast. Original and final weights of plants on nineteen 1-metre-square areas at Port Erin.

The Devon population on the *Fucus serratus* squares was much more nearly a pure *F. serratus* population than that on the Port Erin station. There was no *Ascophyllum* present, and the final weight was only 4·7 kg. short of the original weight.

Other final weights of populations, developed after clearance on the Devon and Argyll coasts, are given in Table XXXII in the Appendix (p. 513).

Fucus serratus *on cut areas*

The results of experiments in which the vegetation was truncated do not differ greatly from those with *F. vesiculosus*. As with the latter species, the areas of *F. serratus* showed normal growth of apices which were too short to be cut. The removal of a large percentage of the apical cells by cutting seems to be detrimental to the tone of the plant. Denudation of the wings of the fronds

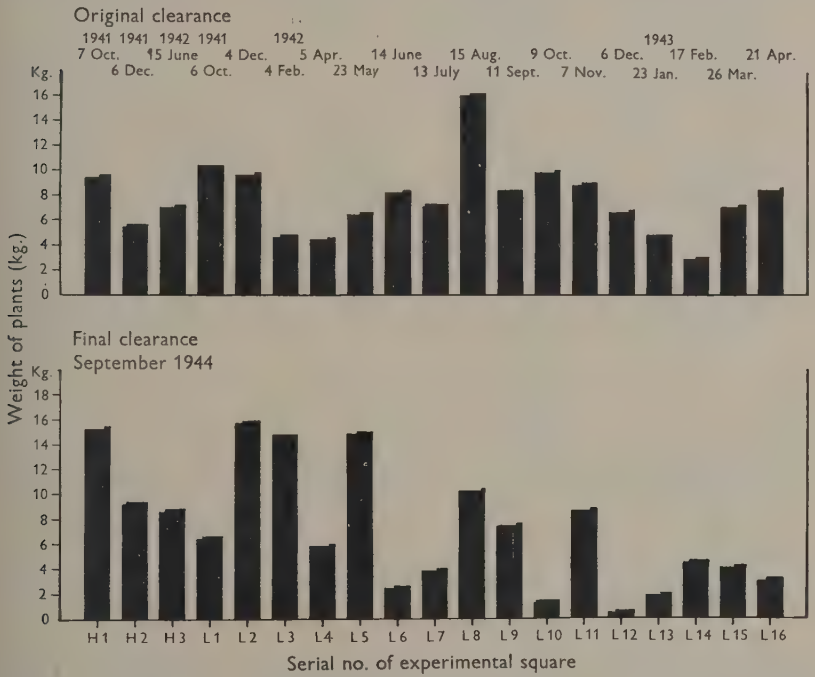

Fig. 32. The repopulation of cleared areas by *Fucus serratus* on the Devon coast. Original and final weights of plants on nineteen 1-metre-square areas at Wembury.

is marked, and the plant is readily infected by epiphytic algae. The growth of the uncut shoots keeps pace with the elongation of young plants which develop on the experimental plots if the original truncation was made at a height of 30 cm. from the base of the plant. When the level of cutting was 15 cm. from the base, the rate of elongation of uncut fronds was less than that of young plants. The explanation of the difference lies in the age of the cut frondage. Cutting at a level of 15 cm. leaves only old portions of large plants. These lower parts of the plant have much less vigour of growth than the younger distal frondage. On cut fronds of *F. serratus* it is only rare that proliferations

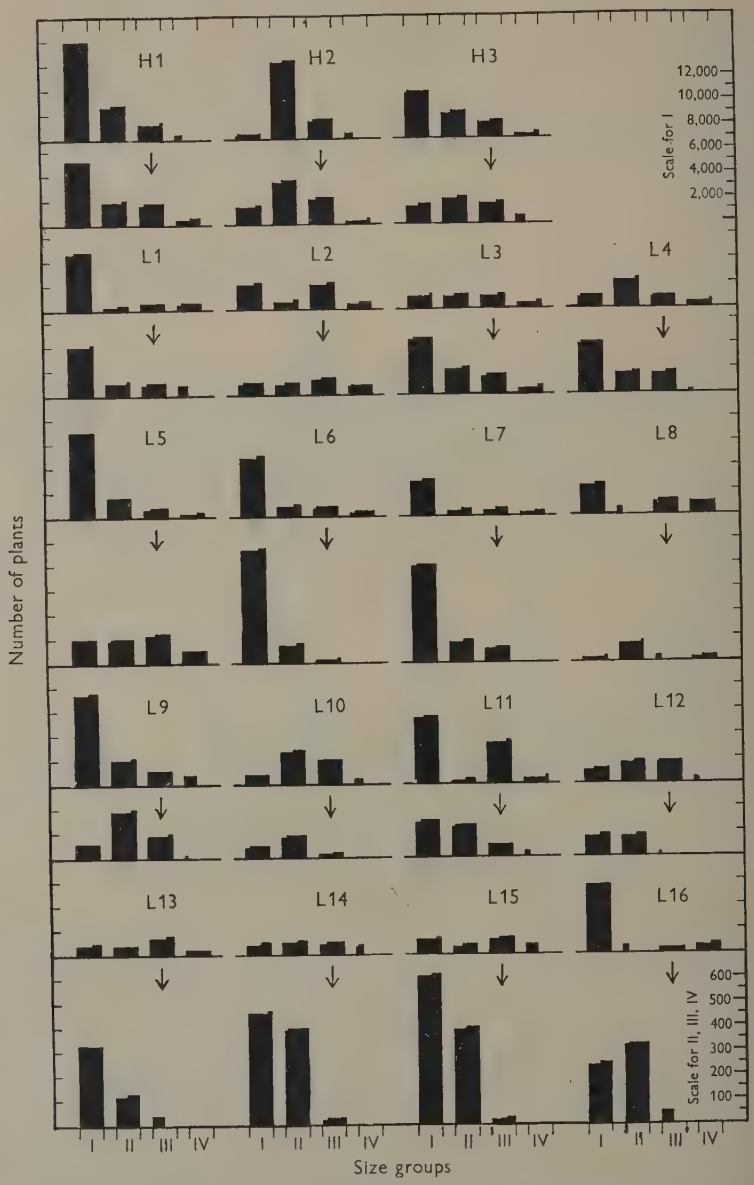

Fig. 33. The repopulation of cleared areas by *Fucus serratus* on the Devon coast. Original and final numbers of plants in size-groups on nineteen 1-metre-square areas at Wembury. Size-groups as follows: I, under 10 cm. in length; II, 10–27 cm.; III, 27–55 cm.; IV, 55 cm. and over. Scale for Group I (top right corner) is reduced by a factor of 20.

occur on the bare midribs or on the cut surfaces of the fronds. In this respect the species differs from *F. vesiculosus* which proliferates readily.

From such experiments in cutting which have been done in this investigation, it would appear that reaping every 2 years would give the best results. There is no advantage in waiting for plants of larger growth because the depletion rate for large plants is too high to permit of any advantage. A good uniform population of young plants develops in one year, but they are very light; the second year population has a greatly increased bulk, but the depletion rate rises. New populations grow very rapidly on cleared areas, and it does not appear that cutting off the tops of the plants rather than removing them bodily would give any advantage, especially with *F. serratus*.

From records which are available it seems that the cutting of fucoids is usually annual, and on the coast of France weed is reaped twice in the year. Whether that is done because there is a better total yield from areas treated in this way or because the weed is needed every year is not stated. The reaping referred to in the literature is probably a mixed crop of *Ascophyllum* and the two species of *Fucus*. No mention is made of how much of the area is reaped at one time. It would appear from the results of the present experiments that the best yield might be gained by reaping alternate areas at intervals of 18 months to 2 years.

Sauvageau (1920) makes reference to the view held by the French weed-cutters that weed reaped in the spring is of greater value as a fertilizer than weed reaped in the autumn. There is no reference to which component of the weed is meant in this statement. In the spring, both *F. vesiculosus* and *Ascophyllum* would be fruiting and might be considered to be in a state of greatest vigour, but this could not apply to *Fucus serratus*. Further research is obviously needed into the seasonal change of chemical content of the weed at various ages, and especially changes related to the onset and development of the reproductive stages.

Conclusion

Concentration on details of seasonal behaviour of two species of marine algae over an extended period of time has revealed some facts which were not known before. The interest of the records lies not only in their novelty, but also in the speculation to which they may give rise.

One is familiar with the alternation of reproductive and vegetative phases in land plants, but with the two species of *Fucus* under discussion, the seasonal rhythms stand opposed to one another; the vegetative season of one coincides with the reproductive season of the other species. The actual physical components of the environment which control the onset of reproduction are as yet unascertained.

It is also somewhat surprising to find that the familiar monopodial and sympodial branching of land plants have their counterparts in the sea; and

that something very like an axial gradient is shown by the basipetally increasing latency of apices in *F. serratus*.

The degree of apical control on subperipheral frondage is also well marked. Apical controls are exerted on the stature of proliferations from various levels in the plant body, and on the arrest of necrosis of tissue following reproduction, at a point where one arm of a dichotomy is still provided with an apical cell. In the development of receptacles an antithesis between vegetative elongation and reproduction is shown by the fact that in *F. vesiculosus* gametangia are not laid down in the receptacle until the apical cell has ceased to function and the apical groove has flattened out.

It is interesting to reflect that in the course of a long evolution in the sea, such relatively 'simple' marine plants as these two species of *Fucus* have developed growth rhythms, habits of branching, controlled defoliation after fruiting, and apical control of remote parts of subtending tissue, in a degree comparable to that shown by land plants with an entirely different history.

Summary

A certain variation in level of the fucoid zone with latitude is demonstrated. The belt of *Fucus vesiculosus* and *F. serratus* lies lower on the Devon coast than on either the Manx or the Argyll coast.

The conditions for the optimum germination of fertilized eggs are dissimilar to those for maximum rate of frond-extension.

Normal growth-rates have been established for both species for the first 3 years of life. In *F. vesiculosus* the average rate of elongation per week is 0·48 cm. on the Devon coast, 0·45 cm. on the Manx coast and 0·68 cm. on the Argyll coast. In *F. serratus* the average rate of elongation per week is 0·49 cm. on the Devon coast, 0·68 cm. on the Manx coast and 0·85 cm. on the Argyll coast. The rate of growth is shown to vary with the conditions of the environment. Shelter from rough water tends to enhance growth-rate, and there is an indication that greater stature is achieved by the plants from the Argyll station than from either of the other stations.

Growth-rate in the second and subsequent years shows a rhythm induced by alternating emphasis on receptacle-formation and frond-extension.

The rate of forking is shown to be encouraged by conditions of exposure, but is unaccountably greater on the Devon coast for both species.

The existence of a morphological rhythm showing latent superiority of growth-potential by one arm of a dichotomy, alternating from side to side of the thallus at each successive dichotomy has been demonstrated.

Continued frond-extension in *F. serratus* has been shown to proceed by a kind of relay-system. Distal frondage becomes largely receptacular and further elongation of the plant is brought about by the renewed activity of subperipheral apices.

Frond-extension in *F. vesiculosus* is due to continued elongation of primary and secondary leaders which may produce reproductive fans in pseudo-lateral positions but always maintain one peripheral leader.

The range of variation shown by *F. vesiculosus* in number and position of vesicles is illustrated and its significance discussed.

The sequence of stages in receptacle-formation is defined. The incidence of fruiting is compared for the two species and for various stations. *Fucus serratus* is shown to have a wider range of fruiting time in relation to geographical locality.

The excision of depleted receptacular frondage is achieved by necrosis of tissue, working basipetally until stopped at a dichotomy, one arm of which is still under the control of a functional apex, however distant.

Depopulation brought about by accidental removal of plants in rough weather is shown to be considerable.

Repopulation in relation to the time factor is discussed on data from the three stations.

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APPENDIX

TABLE IX. GROWTH-RATE BY MARKED PLANTS OF *FUCUS VESICULOSUS* AT WEMBURY

Square 14 on strip

Plant no.	Duration of exp. (days)	Increase in length (cm.)	Increase in no. of dichotomies	Increase in no. of tips	Growth-rate per week (cm.)
A 1	287	26·0	7	517	0·69
2	364	36·0	9	628	0·71
3	512	27·0	9	218	0·36
4	377	40·0	12	1761	0·74
5	338	19·0	9	625	0·36
6	157	19·5	5	—	0·87
7	186	23·5	8	521	0·88
B 1	32	4·5	2	—	1·0
2	32	3·5	1	—	0·75
3	58	6·5	1	—	0·78
4	383	27·0	10	—	0·49
5	58	4·5	4	—	0·52
6	165	8·5	2	—	0·31
C 1	32	7·0	0	—	1·55
2	191	13·0	5	—	0·46
3	58	9·5	2	—	1·14
4	221	7·0	3	—	0·22
5	235	6·0	6	—	0·17
6	134	8·0	1	—	0·41
7	105	3·5	2	—	0·23
8	193	11·5	5	—	0·40

Average elongation-rate, 0·62 cm. per week.

TABLE X. GROWTH-RATE BY MARKED PLANTS OF *FUCUS VESICULOSUS* AT WEMBURY

Square 16A on strip

Plant no.	Duration of exp. (days)	Increase in length (cm.)	Increase in no. of dichotomies	Growth-rate per week (cm.)
1	810	34·0	11	0·29
2	249	19·0	7	0·53
3	633	34·0	17	0·37
4	664	33·0	13	0·34
5	810	56·5	21	0·48
6	563	40·0	10	0·49
7	371	21·5	4	0·40

Average elongation rate, 0·41 cm. per week.

Table XI. Growth-rate by Marked Plants of *Fucus vesiculosus* at Wembury

Fucus vesiculosus, areas 1 and 2

Plant no.	Length (cm.) Initial	Final	Increase	No. of dichotomies Initial	Final	Duration of exp. in days	Growth-rate per week (cm.)
Area 1: 725	34·0	31·0 F.	−3·0	9	9	931	—
		48·0 M.	14·0	9	12	461	0·21
727	36·0	54·0	18·0	9	26	688	0·18
284	9·0	35·0	26·0	2	13	654	0·26
705	46·0	71·0	15·0	18	24	546	0·32
710	22·0	35·5	13·5	6	11	490	0·19
726	16·0	27·5	11·5	5	8	385	0·20
740	26·0	55·0	29·0	6	20	654	0·31
707	44·0	51·0	7·0	16	15	210	0·23
708	24·0	31·5	7·5	10	18	325	0·16
720	45·0	56·0	11·0	17	23	210	0·36
724	22·0	32·5	10·0	5	9	325	0·21
728	43·0	62·5	19·5	11	21	268	0·50
742	29·0	33·0	4·0	5	10	325	0·08
743	48·0	72·0	24·0	11	24	414	0·40
744	38·0	55·0	17·0	14	20	325	0·36
750	44·0	59·5	15·5	18	25	268	0·40
150	18·0	20·5	2·5	3	4	210	0·08
151	14·5	17·8	3·3	1	1	182	0·12
Area 2: 1	82·0	96·0	14·0	32	37	309	0·29
8	71·0	81·0	10·0	21	24	183	0·38
11	76·5	79·0	2·5	27	29	94	0·17
16	67·0	70·0	3·0	24	24	94	0·22
17	71·5	85·0	13·5	18	21	183	0·51
72	13·0	28·5	15·5	3	8	324	0·33
82	25·0	46·0	21·0	6	16	385	0·38
86	46·0	54·0	8·5	12	17	309	0·17
88	26·5	51·0	24·5	7	15	324	0·52
4	49·5	87·0	37·5	15	26	619	0·42
5	37·0	66·0	29·0	14	25	619	0·32
22	50·0	66·0	16·0	15	22	619	0·18
14	75·0	103·0	28·0	19	32	493	0·39
13	104·0	114·5	10·5	33	41	124	0·59
64	19·5	67·0	47·5	4	20	619	0·53
65	61·0	99·0	38·0	19	33	493	0·53
66	38·5	82·0	43·5	6	22	619	0·49
77	28·0	43·0	15·0	9	14	428	0·24
83	19·5	31·0	11·5	4	9	435	0·18
90	69·0	75·0	6·0	20	19	156	0·26
91	59·0	91·0	32·0	14	31	588	0·38
3	38·0	73·0	35·0	13	24	543	0·45
9	73·0	81·5	8·5	22	27	183	0·32
20	59·0	63·5	4·5	21	22	94	0·33
63	34·5	61·5	27·0	8	16	566	0·33
21	47·0	51·5	4·5	14	17	222	0·14
80	30·0	49·0	19·0	7	17	320	0·41

Average elongation rate, 0·31 cm. per week.

TABLE XII. GROWTH-RATE BY MARKED PATCHES OF *FUCUS VESICULOSUS* AT WEMBURY

Square 16 A on strip, patches 1–3. December 1941 to April 1943

	Date ...	1941 4 Dec.	1942 2 Feb.	3 Apr.	13 May	15 June	15 July	16 Aug.	12 Sept.
1.	Length (cm.)	<1·0– 8·0	<1·0–11·2	<1·0–13·5	<1·0–17·5	<1·0–20·2	—	<1·0–32·0	<1·0–35·0
	No. of dichotomies	0–1	0–4	0–4	0–5	0–6	—	0–8	0–8
2.	Length (cm.)	<1·0–10·0	1·0–12·5	1·0–13·0	<1·0–16·7	<1·0–19·0	<1·0–20·5	<1·0–28·0	<1·0–31·0
	No. of dichotomies	0–4	0–5	0–4	0–5	0–6	0–6	0–8	0–10
3.	Length (cm.)	<1·0–18·0	<1·0–23·0	<1·0–16·0	<1·0–19·5	<1·0–23·0	<1·0–26·0	<1·0–29·0	<1·0–35·0
	No. of dichotomies	0–7	0–10	0–4	0–5	0–7	0–7	0–8	0–8

	Date ...	1942 13 Oct.	9 Nov.	12 Dec.	1943 22 Jan.	19 Feb.	3 Mar.	4 Apr.
1.	Length (cm.)	<1·0–37·0	<1·0–39·5	<1·0–42·0	<1·0–38·5	<1·0–40·0	<1·0–42·0	—
	No. of dichotomies	0–9	0–11	0–10	0–8	0–11	0–10	—
2.	Length (cm.)	<1·0–34·0	<1·0–35·0	<1·0–36·5	<1·0–27·0	<1·0–36·0	<1·0–40·0	<1·0–42·5
	No. of dichotomies	0–11	0–12	0–12	0–13	0–11	0–12	0–11
3.	Length (cm.)	<1·0–36·0	<1·0–33·0	<1·0–45·0				
	No. of dichotomies	0–12	0–10	0–9				

TABLE XIII. GROWTH-RATE BY MARKED PATCHES OF *FUCUS VESICULOSUS* AT WEMBURY

Fucus vesiculosus area, patches 1–4. December 1941 to April 1943

	Date ...	1941 16 Dec.	1942 5 Feb.	18 Apr.	15 May	16 June	14 July	13 Aug.	10 Sept.
1.	Length (cm.)	0·5– 3·0	<1·0– 5·2	<1·0– 7·0	<1·0–13·0	<1·0–13·0	<1·0–18·0	<1·0–22·0	<1·0–25·0
	No. of dichotomies	0–1	0–1	0–1	0–2	0–2	0–4	0–6	0–5
2.	Length (cm.)	0·5– 5·0	<1·0– 6·0	<1·0–10·0	<1·0–11·0	<1·0–14·8	<1·0–19·0	<1·0–20·5	<1·0–26·5
	No. of dichotomies	0–1	0–2	0–2	0–3	0–3	0–5	0–4	0–8
3.	Length (cm.)	<1·0–11·5	<1·0–11·5	<1·0–15·5	<1·0–18·5	<1·0–20·0	<1·0–21·5	<1·0–23·0	<1·0–26·0
	No. of dichotomies	0–3	0–3	0–3	0–4	0–6	0–7	0–7	0–7
4.	Length (cm.)	<1·0– 9·5	<1·0–13·5	<1·0–17·0	—	<1·0–24·5	<1·0–28·0	2·0–34·0	2·5–35·0
	No. of dichotomies	0–2	0–2	0–4	—	0–5	0–6	0–10	0–9

	Date ...	1942 8 Oct.	6 Nov.	5 Dec.	1943 5 Jan.	2 Feb.	21 Mar.	20 Apr.
1.	Length (cm.)	<1·0–27·5	<1·0–27·0	<1·0–23·0	<1·0–23·5	<1·0–32·0	<1·0–33·5	<1·0–38·0
	No. of dichotomies	0–7	0–8	0–7	0–7	0–9	0–8	0–12
2.	Length (cm.)	<1·0–29·5	<1·0–32·0	<1·0–34·0	<1·0–34·0	<1·0–35·5	<1·0–35·5	<1·0–40·0
	No. of dichotomies	0–9	0–11	0–12	0–13	0–12	0–11	0–13
3.	Length (cm.)	<1·0–25·5	<1·0–29·0	<1·0–27·0	<1·0–30·0	<1·0–34·5	<1·0–30·0	<1·0–32·0
	No. of dichotomies	0–7	0–8	0–9	0–10	0–11	0–12	0–14
4.	Length (cm.)	6·5–40·0	5·5–41·0	6·0–42·5	7·0–49·0	1·0–51·5	7·0–52·0	13·0–55·0
	No. of dichotomies	0–9	0–9	0–8	0–12	0–12	0–12	0–11

TABLE XIV. GROWTH-RATE OF *FUCUS VESICULOSUS* BY CLEARED AREA METHOD AT WEMBURY

Metre squares 1–16

Square no.	Period of exp. (years + days)	Growth-rate for 1 year (cm. per week)	Growth-rate for whole period (cm. per week)
1	2 y. 193 d.	0·59	0·54
2	2 y. 175 d.	0·46	0·41
3	2 y. 144 d.	0·28	0·39
4	2 y. 126 d.	0·51	0·42
5	2 y. 92 d.	0·53	0·54
6	2 y. 289 d.	0·41	0·42
7	2 y. 259 d.	0·46	0·40
8	2 y. 200 d.	0·25	0·32
9	2 y. 208 d.	0·37	0·53
10	2 y. 179 d.	0·38	0·57
11	2 y. 150 d.	0·42	0·51
12	2 y. 112 d.	0·43	0·48
13	2 y. 83 d.	0·49	0·56
14	2 y. 49 d.	0·42	0·53
15	2 y. 22 d.	0·49	0·48
16	2 y. 10 d.	0·41	0·47

Average elongation-rate for 1 year, 0·43 cm. per week.
Average elongation-rate for whole period, 0·47 cm. per week.

TABLE XV. GROWTH-RATE OF *FUCUS VESICULOSUS* BY CLEARED AREA METHOD IN THE ISLE OF MAN

Port Erin, strip 1

Square no.	Length of plants (cm.) 1941 Aug.	1942 Jan.	Apr.	Aug.	Dec.	1943 Apr.	Growth-rate per week (cm.) 1st year	1 yr. 9 months
−7	Cleared	12·0	19·0	27·5	31·0	34·5	0·51	0·40
−5	Cleared	9·0	14·3	26·0	33·5	42·5	0·48	0·49
−2	Cleared	3·0	11·5	20·0	30·5	41·5	0·37	0·48
−1	Cleared	10·5	15·5	25·0	35·0	43·0	0·46	0·49
1	Cleared	4·5	11·0	18·0	25·0	37·0	0·34	0·43
2	Cleared	10·5	14·0	19·0	28·5	39·5	0·37	0·46
3	Cleared	5·0	10·0	14·5	21·0	27·0	0·39	0·31
4	Cleared	5·0	11·0	14·5	20·5	29·0	0·29	0·33
5	Cleared	7·0	17·5	24·5	31·5	42·5	0·45	0·49
10	Cleared	16·0	28·5	39·0	43·5	49·5	0·74	0·57

Average elongation-rate, 0·45 cm. per week.

TABLE XVI. GROWTH-RATE OF *FUCUS VESICULOSUS* BY CLEARED AREA METHOD IN ARGYLL. SGEIR BHUIDHE AND LOBSTER POND

Station: Sgeir Bhuidhe (exposed locality)

Length in cm.

1942					1943					1944	
Mar.	June	July	Sept.	Nov.	Feb.	Apr.	June	Aug.	Oct.	Feb.	Sept.
Cleared	—	2·1	7·0	11·0	16·0	19·0	23·5	22·0	24·0	32·5	41·0

Station: Lobster Pond (sheltered locality)

Length in cm.

1942				1943		1944	
Feb.	June	Sept.	Nov.	Feb.	Aug.	Feb.	Sept.
Cleared	3·0	7·0	20·0	29·0	46·0	58·0	77·0

TABLE XVII. GROWTH-RATE OF *FUCUS VESICULOSUS* BY CLEARED AREA METHOD IN ARGYLL. ASCOPHYLLUM ROCK

West strip	Duration of exp. (days)	Increase in length (cm.)	Growth-rate per week (cm.)
Upper level	969	100	0·72
Middle level	969	119	0·86
Low level	969	90	0·65
Area 3	569	68	0·83
East Strip	819	110	0·93
Square AH1	495	28	0·28
Square AH2	495	36	0·51

Average growth-rate for the area is 0·68 cm. per week.

TABLE XVIII. GROWTH-RATE BY MARKED PLANTS OF *FUCUS SERRATUS* AT WEMBURY

Square 15 on strip

Plant no.	Duration of exp. (days)	Increase in length (cm.)	Increase in no. of dichotomies	Increase in no. of tips	Growth-rate per week (cm.)
A 1	221	17·5	6	305	0·55
2	273	19·0	5	86	0·50
3	532	36·5	12	1639	0·48
4	532	39·0	11	1929	0·51
5	243	16·0	5	373	0·46
6	348	30·5	10	—	0·61
7	253	13·0	3	156	0·36
					Av. 0·50
B 1	199	23·5	7	256	0·83
2	59	5·8	1	31	0·68
3	59	6·5	1	7	0·77
4	570	19·5 max.	7	499	0·24
5	257	18·0 unbroken	4	379	0·49
6	119	12·0	2	83	0·70
7	550	17·0	7	46	0·21
8	246	16·0 unbroken	6	52	0·37
9	30	3·0	0	—	0·70
					Av. 0·55
C 1	59	5·0	2	75	0·49
2	59	5·0	0	17	0·49
3	29	1·5	1	—	0·36
4	539	45·5	11	1696	0·59
5	119	13·0	2	77	0·76
6	217	15·5	3	51	0·50
7	495	31·0	10	488	0·44
8	539	45·5	11	1908	0·59
					Av. 0·53
D 1	155	16·5	3	47	0·74
2	59	2·5	1	15	0·29
3	549	7·5	4	575	0·09
4	257	12·5 unbroken	4	260	0·34
5	296	4·0	3	—	0·09
6	199	6·0	2	—	0·18
7	59	2·5	0	17	0·29
8	227	21·0	5	173	0·61
9	199	22·0 unbroken	4	—	0·74
10	270	15·0	6	181	0·38
11	199	16·0 unbroken	4	137	0·56
12	199	20·5	4	275	0·71
					Av. 0·42
E 1	298	7·5	2	−18	0·13
2	228	17·5 unbroken	3	34	0·40
3	518	38·5	10	152	0·52
4	313	27·5 unbroken	7	261	0·64
5	149	14·5	4	185	0·68
6	518	22·5	10	140	0·30
7	270	19·0 unbroken	7	156	0·49
8	417	18·0	5	51	0·30
9	270	27·5	9	225	0·71
10	228	24·0	6	546	0·73
11	518	45·0	12	416	0·57
12	383	16·5	6	41	0·35
					Av. 0·49
F 1	143	16·5	7	272	0·80
2	193	17·5	4	164	0·63
3	59	7·0	1	10	0·83
4	544	60·0	14	419	0·77
5	291	6·5	1	15	0·15
6	544	38·5	12	1386	0·49
7	544	35·5	10	409	0·45
8	544	34·5	13	220	0·44
					Av. 0·57

Average elongation rate, 0·50 cm. per week.

Table XIX. Growth-rate by Marked Plants of *Fucus serratus* at Wembury

Square 21 on strip

Plant no.	Length (cm.) Initial	Final	Increase	No. of dichotomies Initial	Final	Duration of exp. (days)	Growth-rate per week (cm.)
1	14·0	51·0 F.	37·0	6	23	989	0·26
		52·0 M.	38·0	—	—	727	0·36
2	28·0	80·0	52·0	9	25	989	0·36
3	13·5	61·0	47·5	6	23	989	0·33
4	8·0	70·0	62·0	3	25	989	0·43
5	14·0	62·5	45·5	5	21	989	0·32
6	13·5	51·5	38·0	6	20	606	0·44
7	25·0	36·5	11·5	9	12	338	0·23
8	9·5	12·0	2·5	4	6	281	0·06
9	13·0	42·0	29·0	4	12	309	0·65
10	12·0	32·5	20·5	3	10	309	0·42
11	36·0	64·0	28·0	11	16	309	0·63
12	14·0	28·5	14·5	6	12	212	0·47
13	20·0	40·0	20·0	6	15	338	0·41
14	11·0	31·0	20·0	4	9	311	0·45
15	8·0	27·0	19·0	3	8	254	0·52
16	10·0	14·2	4·2	5	8	163	0·18
17	10·5	30·8	20·3	3	8	254	0·56
18	11·5	34·0	22·5	2	8	281	0·56
19	7·5	41·0	33·5	2	13	415	0·56
20	9·0	27·5	18·5	5	11	254	0·50
21	14·5	39·5	25·0	4	10	338	0·51
22	14·0	40·0	26·0	4	11	338	0·53
23	7·5	37·0	29·5	3	12	338	0·61
24	6·0	34·0	28·0	2	10	373	0·52

Average elongation-rate, 0·43 cm. per week.

Table XXI. Growth-rate by Marked Plants of *Fucus serratus* at Wembury

Square 16 on strip

Plant no.	Length (cm.) Initial	Final	Increase	No. of dichotomies Initial	Final	Duration of exp. (days)	Growth-rate per week (cm.)
165	12·5	39·0	26·5	5	16	824	0·22
303	8·0	45·0	37·0	3	17	764	0·33
288	13·5	66·0	52·5	6	26	943	0·39
301	9·5	48·0	38·5	3	15	635	0·42
167	10·0	59·5	49·5	3	21	855	0·40
160	14·0	39·5	25·5	5	14	372	0·48
168	14·5	19·5	5·0	5	8	303	0·11
171	14·0	38·5	24·5	5	14	372	0·46
173	11·0	38·0	27·0	4	11	372	0·48
175	17·0	38·5	21·5	8	13	271	0·55
294	9·0	27·5	18·5	3	9	253	0·51
297	12·0	28·5	16·5	5	10	253	0·45
298	10·5	33·5	23·0	5	12	372	0·44
304	10·5	44·0	33·5	6	15	635	0·36
305	6·0	17·0	11·0	2	10	532	0·14
307	7·5	29·5	22·0	2	11	342	0·45
308	6·0	30·0	24·0	1	10	342	0·49
438	7·5	26·0	18·5	2	9	253	0·51
170	17·0	31·0	14·0	6	11	222	0·44

Average elongation-rate, 0·40 cm. per week.

TABLE XX. GROWTH-RATE BY MARKED PLANTS OF *FUCUS SERRATUS* AT WEMBURY

Square 21 *a* on strip

Plant no.	Length (cm.) Initial	Final	Increase	No. of dichotomies Initial	Final	Duration of exp. (days)	Growth-rate per week (cm.)
196	25·0	40·5	15·5	7	13	314	0·33
197	20·0	37·0	17·0	8	13	369	0·32
335	12·0	19·5 F.	7·5	4	10	989	0·05
		21·0 M.	9/0	4	7	504	0·11
336	9·0	45·5	36·5	3	14	534	0·47
337	10·0	29·0	19·0	5	12	369	0·35
338	10·5	47·0	36·5	4	16	534	0·47
339	14·9	57·0	43·0	4	16	608	0·49
340	16·0	31·5	15·5	6	10	806	0·13
342	14·0	43·5	29·5	5	14	899	0·22
343	12·0	22·5	10·5	3	6	193	0·37
346	11·5	69·0	57·5	5	22	945	0·42
347	11·0	63·0	52·0	3	19	989	0·36
348	8·0	44·0	32·0	3	17	989	0·22
349	8·0	61·0	53·0	3	19	989	0·37
450	7·5	48·5	41·0	2	16	945	0·30
651	36·0	50·5	14·5	9	18	669	0·15
654	39·0	68·0	25·0	4	19	256	0·68
657	63·0	78·0	15·0	16	28	324	0·32
661	44·0	63·0	19·0	12	21	504	0·26
662	51·0	70·0	19·0	14	22	441	0·30
664	37·0	71·0	34·0	10	21	534	0·44
27	29·0	56·5	27·5	11	19	669	0·28
28	35·5	49·0	13·5	10	15	282	0·33
29	36·5	42·0 F.	6·5	12	15	799	0·05
		58·0 M.	21·5	12	18	222	0·67
34	79·0	92·0	13·0	18	26	256	0·35
35	28·0	64·5	36·5	9	23	608	0·42
36	64·0	77·0	13·0	14	20	256	0·35
41	45·0	56·5	11·5	18	21	256	0·31
42	41·0	48·0	7·0	11	13	256	0·19
43	71·0	89·0 F.	19·0	14	22	256	0·52
		90·0 M.	18·0	14	21	369	0·34
45	53·0	71·5 F.	18·5	14	19	256	0·50
		75·0 M.	22·0	14	22	560	0·27
46	40·0	54·0 F.	37·5	12	27	945	0·27
		77·5 M.	14·0	12	20	416	0·23
48	39·0	52·5 F.	21·0	14	20	608	0·23
		60·0 M.	13·5	14	18	324	0·29
200	24·0	70·0	46·0	8	20	608	0·53
201	11·5	42·5	31·0	5	14	608	0·35
202	22·0	61·5	39·5	8	18	560	0·43
203	20·5	25·5	15·5	6	9	282	0·38
205	16·0	75·0	59·0	5	23	945	0·43
206	20·0	47·0	27·0	6	12	728	0·26
209	20·5	14·5	4·0	6	12	369	0·07
210	22·5	51·0	28·5	8	14	534	0·37
212	25·5	61·0	35·5	10	20	504	0·49
213	20·0	29·5	9·5	6	10	369	0·17
215	33·0	61·0	28·0	10	14	369	0·53
216	35·5	58·0	22·5	12	19	369	0·42
217	31·0	68·0	37·0	11	18	608	0·42
218	32·0	60·0	28·0	12	17	504	0·38
220	33·0	50·0	17·0	10	14	369	0·32
221	27·0	44·5	17·5	11	16	343	0·36
222	25·0	48·5	23·5	10	17	534	0·30
223	26·0	50·0	24·0	10	16	416	0·40
224	29·0	49·0	20·0	11	16	669	0·21
225	24·5	55·0	30·5	7	17	638	0·33
227	38·0	73·0	35·0	8	19	560	0·53
230	25·0	56·0	31·0	9	17	369	0·58
234	29·0	53·5	24·5	9	19	324	0·43
236	20·5	32·5	12·0	7	10	369	0·22
239	20·0	35·0	15·0	6	11	369	0·28
241	23·0	64·0	41·0	8	21	638	0·45
242	17·0	60·0	43·0	6	20	669	0·45
244	21·5	52·5	31·0	7	17	608	0·35
245	12·5	39·5	27·0	6	15	369	0·51
247	21·0	42·5	21·5	8	15	416	0·35
249	12·0	19·0	7·0	5	7	416	0·11
250	13·0	61·0	48·0	5	21	989	0·34

F., final. M., maximum.

Average elongation-rate, 0·35 cm. per week.

Table XXII. Growth-rate by Marked Patches of *Fucus serratus* at Wembury

Square 16 on strip, patches 1–4. December 1941 to April 1943

Date ...	1941 22 Dec.	1942 2 Feb.	3 Apr.	13 May	14 June	15 July	15 Aug.	12 Sept.
1. Length (cm.)	0·2– 1·0	1·2– 2·0	4·0– 6·0	5·0– 8·5	1·0–10·5	1·0–12·5	1·0–20·0	1·0–20·5
No. of dichotomies	0	0	0–1	1–2	0–3	0–4	0–5	0–7
2. Length (cm.)	< 1·0– 3·5	< 1·0– 3·8	1·0– 9·0	< 1·0–11·5	< 1·0–15·5	< 1·0–16·0	< 1·0–20·0	< 1·0–21·0
No. of dichotomies	0–1	0–2	0–3	0–4	0–6	0–6	0–6	0–7
3. Length (cm.)	1·0– 5·0	1·0– 8·0	1·0–12·0	1·0–14·5	1·0–15·5	1·5–19·5	1·0–24·5	1·0–26·0
No. of dichotomies	0–1	0–3	0–5	0–5	0–5	0–7	0–7	0–8
4. Length (cm.)	1·0– 9·0	1·0–11·2	1·0–15·5	1·0–20·0	1·0–23·0	1·0–20·5	1·0–27·0	1·0–31·0
No. of dichotomies	0–2	0–4	0–6	0–8	0–7	0–7	0–8	0–8

Date ...	1942 13 Oct.	12 Nov.	12 Dec.	1943 22 Jan.	7 Feb.	21 Mar.	22 Apr.
1. Length (cm.)	1·0–21·0	< 1·0–22·0	< 1·0–22·0	< 1·0–32·0	< 1·0–23·5	< 1·0–34·0	< 1·0–25·0
No. of dichotomies	0–7	0–8	0–8	0–9	0–8	0–11	0–9
2. Length (cm.)	< 1·0–22·0	< 1·0–22·0	< 1·0–20·5	< 1·0–21·5	< 1·0–21·5	< 1·0–24·5	< 1·0–28·5
No. of dichotomies	0–8	0–8	0–8	0–9	0–9	0–8	0–7
3. Length (cm.)	2·0–29·5	1·0–30·0	1·0–34·0	1·0–37·0	1·0–38·5	1·0–39·5	1·0–43·0
No. of dichotomies	0–9	0–10	0–11	0–12	0–11	0–11	0–13
4. Length (cm.)	1·0–33·8	1·0–35 5	1·0–36·0	1·0–33·5	1·0–35·5	1·0–35·5	1·0–37·0
No. of dichotomies	0–9	0–10	0–11	0–10	0–12	0–11	0–12

Table XXIII. Growth-rate by Marked Patches of *Fucus serratus* at Wembury

Square 21 on strip, patches 1–3. December 1941 to April 1943

Date ...	1941 4 Dec.	1942 2 Feb.	5 Apr.	16 May	15 June	15 July	15 Aug.	12 Sept.
1. Length (cm.)	0·5– 1·5	1·4– 2·0	3·0– 5·0	1·0–10·0	1·0–11·2	1·0–15·5	1·0–20·0	1·0–21·5
No. of dichotomies	0	0	0–1	1–2	1–3	0–4	0–5	0–5
2. Length (cm.)	0·5– 1·5	1·6– 2·2	1·0– 6·5	1·0– 9·0	1·0–10·5	1·0–13·5	1·0–20·0	1·0–25·0
No. of dichotomies	0	0	0–2	0–3	0–3	0–4	0–6	0–9
3. Length (cm.)	1·0– 9·0	1·0– 9·0	1·0–12·0	—	1·0–19·5	1·0–23·0	1·0–31·0	1·0–31·0
No. of dichotomies	1–2	2–3	0–3	—	0–6	0–8	0–8	0–8

Date ...	1942 9 Oct.	11 Nov.	12 Dec.	1943 21 Jan.	18 Feb.	21 Mar.	22 Apr.
1. Length (cm.)	1·0–25·0	1·0–26·5	1·0–31·5	1·0–27·5	1·0–29·5	1·0–31·0	1·0–22·0
No. of dichotomies	0–7	0–7	0–8	0–8	0–9	0–10	0–7
2. Length (cm.)	1·0–25·0	1·0–25·5	1·0–28·0	1·0–28·5	1·0–26·0	1·0–25·5	1·0–23·0
No. of dichotomies	0–9	0–9	0–9	0–9	0–9	0–9	0–9
3. Length (cm.)	1·0–33·5	1·0–35·0	1·0–38·0	1·0–38·0	1·0–38·0	1·0–38·0	1·0–44·0
No. of dichotomies	0–10	0–11	0–12	0–13	0–11	0–13	0–13

Table XXIV. Growth-rate by Marked Patches of *Fucus serratus* at Wembury

Square 22 on strip. December 1941 to April 1943

Date ...	1941 12 Dec.	1942 4 Feb.	2 Apr.	16 May	15 June	15 July	15 Aug.	12 Sept.
Length (cm.)	0·2– 2·4	1·0– 3·1	1·0– 5·5	1·0– 8·0	1·0–11·0	1·0–15·5	1·0–19·0	1·0–21·5
No. of dichotomies	0	0	0–1	0–2	0–4	0–5	0–5	0–6

Date ...	1942 9 Oct.	9 Nov.	12 Dec.	1943 23 Jan.	18 Feb.	13 Mar.	22 Apr.
Length (cm.)	1·0–24·5	1·0–29·0	1·0–32·5	1·0–31·0	1·0–33·0	1·0–32·0	1·0–36·0
No. of dichotomies	0–10	0–9	0–9	0–10	0–10	0–12	0–12

Table XXV. Growth-rate of *Fucus serratus* by Cleared Area Method at Wembury

Metre squares H 1–3, L 1–16

Square no.	Period (days)	Growth-rate per week (cm.)	Period (days)	Growth-rate per week (cm.)	Total period (years + days)	Growth-rate per week (cm.)
H 1	372	0·57	728	0·51	2 y. 331 d.	0·56
2	365	0·49	733	0·82	2 y. 287 d.	0·51
3	367	0·46	725	0·55	2 y. 97 d.	0·60
L 1	368	0·57	755	0·44	2 y. 346 d.	0·50
2	368	0·70	727	0·64	2 y. 309 d.	0·62
3	379	0·60	735	0·60	2 y. 226 d.	0·56
4	381	0·34	733	0·40	2 y. 179 d.	0·45
5	373	0·60	728	0·62	2 y. 142 d.	0·57
6	371	0·34	729	0·42	2 y. 100 d.	0·41
7	383	0·39	724	0·55	2 y. 78 d.	0·46
8	353	0·44	738	0·57	2 y. 35 d.	0·63
9	356	0·47	749	0·57	—	—
10	387	0·52	711	0·43	—	—
11	358	0·60	683	0·65	—	—
12	360	0·23	656	0·32	—	—
13	356	0·74	616	0·67	—	—
14	357	0·54	583	0·55	—	—
15	353	0·43	553	0·62	—	—
16	370	0·46	516	0·58	—	—

Average elongation-rate: Plants approximately 1 year old, 0·50 cm. per week.
Plants 1–2 years old, 0·55 cm. per week.
Plants 2–3 years old, 0·53 cm. per week.

Table XXVI. Growth-rate of *Fucus serratus* and *Fucus vesiculosus* by Cleared Area Method at Wembury

Square 19 on strip

Date	*F. vesiculosus* Length	*F. vesiculosus* No. of dichotomies	*F. serratus* Length	*F. serratus* No. of dichotomies
5. iv. 42	Rock surface removed			
28. iv. 42	No repopulation			
13. v. 42	0·5– 1·0	0	0·5– 1·0	0
17. vi. 42	0·1– 4·0	1	0·1– 4·0	1
15. vii. 42	0·1– 4·0	1	0·1– 4·0	1
14. viii. 42	0·1– 4·0	1	0·1– 4·0	1
13. ix. 42	0·1– 7·0	2	0·1– 7·0	1
14. x. 42	0·1–12·0	2	0·1– 9·2	4
26. x. 42	0·1–14·5	4	—	—
12. xi. 42	0·1–16·3	3	—	—
8. xii. 42	0·1–20·5	5	0·1–12·0	4
21. i. 43	0·1–17·5	4	0·1–16·6	6
18. ii. 43	0·1–15·5	4	0·1–15·0	6
21. iii. 43	0·1–19·0	4	0·1–20·0	6
22. iv. 43	0·1–20·0	6	0·1–24·5	7
22. v. 43	0·1–24·3	6	0·1–23·0	5
16. vi. 43	0·1–26·5	5	0·1–30·5	9
31. vii. 43	0·1–32·0	5	0·1–35·5	9
1. ix. 43	0·1–36·0	6	0·1–36·0	11
3. x. 43	0·1–42·5	8	0·1–40·0	11
1. xi. 43	0·1–45·0	11	0·1–47·5	13
9. xii. 43	0·1–49·0	10	0·1–49·0	10
10. i. 44	0·1–47·0	10	0·1–47·0	12
9. ii. 44	0·1–43·0	12	0·1–52·0	12
14. iii. 44	0·1–46·5	16	0·1–53·0	13
9. iv. 44	0·1–49·0	16	0·1–55·0	14
11. v. 44	0·1–50·0	9	0·1–60·0	16
7. vi. 44	0·1–46·5	13	0·1–64·0	16
6. vii. 44	0·1–58·0	13	0·1–62·5	14
22. viii. 44	0·1–62·0	17	0·1–72·0	16

Average elongation-rate over a period of 2 years 129 days: *F. vesiculosus*, 0·50 cm. per week. *F. serratus*, 0·58 cm. per week.

TABLE XXVII. GROWTH-RATE OF *FUCUS SERRATUS* BY CLEARED AREA METHOD AT WEMBURY

Square 19A 2 on strip

Date	Length (cm.)		No. of dichotomies	
	Plants on rock	Plants on edge of pool	Plants on rock	Plants on edge of pool
9. ix. 41	Rock surface scraped			
6. x. 41	< 1– 2·0			
8. x. 41	Rock surface removed			
17. xi. 41	No repopulation			
4. xii. 41	No repopulation			
30. iii. 42	< 1– 2·0	—	0	—
13. v. 42	1– 5·0	—	1	—
15. vi. 42	1– 8·0	—	2	—
15. vii. 42	1–12·5	1–20·5	3	5
14. viii. 42	1–14·0	1–23·0	7	7
13. ix. 42	1–16·0	1–26·0	6	7
14. x. 42	1–17·7	1–31·0	7	8
9. xi. 42	1–23·5	1–32·5	6	8
12. xii. 42	1–29·0	1–36·0	10	8
21. i. 43	1–24·0	1–38·0	7	9
18. ii. 43	1–34·0	1–37·0	8	9
21. iii. 43	1–31·0	1–34·0	9	9
24. iv. 43	1–30·0	1–43·0	9	10
22. v. 43	1–36·0	1–45·0	10	10
16. vi. 43	1–38·0	1–50·0	10	9
5. viii. 43	1–45·0	—	10	—
1. ix. 43	1–46·0	1–55·0	12	12
3. x. 43	1–48·0	—	8	—
1. xi. 43	1–52·0	—	15	—
9. xii. 43	1–49·0	—	14	—
10. i. 44	1–50·0	—	16	—
12. ii. 44	1–55·0	—	16	—
9. iv. 44	1–60·0	—	16	—
11. v. 44	1–54·0	—	17	—
7. vi. 44	1–56·0	—	16	—
6. vii. 44	1–72·0	—	19	—
22. viii. 44	1–76·0	—	20	—

Average elongation-rate over period of 2 years 348 days: 0·49 cm. per week.
Average elongation-rate of plants near pool over period of 722 days: 0·53 cm. per week.

TABLE XXVIII. GROWTH-RATE OF *FUCUS SERRATUS* BY CLEARED AREA METHOD IN THE ISLE OF MAN

Port Erin Bay, strips 1–3

Strip 1. August 1941 to September 1944

Square no.	Length of plants (cm.) 1941 5 Aug.	1942 2 Jan.	19 Apr.	7 July	1943 10 Dec.	16 Apr.	20 Sept.	1944 1 Jan.	15 Apr.	Rate of growth per week (cm.)
10	Cleared	8·0	16·0	28·5	30·5	38·0	—	—	—	0·43
11	Cleared	8·5	15·0	26·0	38·5	44·5	53·5	—	76·0	0·63
12	Cleared	3·0	11·5	19·0	32·0	41·0	45·0	—	68·0	0·56
13	Cleared	7·5	12·5	14·0	39·5	50·0	41·0	38·0	64·0	0·53
14	Cleared	11·0	14·5	20·5	27·5	31·0	45·0	45·0	69·0	0·57
15	Cleared	9·0	16·0	25·0	28·0	29·0	32·0	50·0	73·0	0·60
16	Cleared	7·5	18·5	25·0	30·0	36·5	60·5	65·0	60·5	0·50
17	Cleared	11·0	20·5	29·5	31·5	37·0	51·0	57·0	73·0	0·60
18	Cleared	13·5	19·0	36·0	42·0	36·5	50·0	61·0	78·0	0·64
19	Cleared	14·5	19·5	30·0	39·0	43·0	59·0	66·5	77·5	0·64
20	Cleared	11·5	20·0	30·5	34·0	38·0	58·0	63·0	75·5	0·64
21	Cleared	6·5	16·0	31·0	38·5	43·0	62·5	50·0	78·5	0·65
22	Cleared	14·0	22·0	31·5	40·0	50·0	48·5	57·0	71·0	0·58
23	Cleared	10·0	21·0	31·0	37·5	48·0	42·0	54·5	61·5	0·51
24	Cleared	8·5	16·0	27·0	32·5	37·0	43·0	55·0	76·0	0·63
25	Cleared	3·0	6·0	16·0	25·0	34·5	—	—	64·0	0·53
26	Cleared	7·5	15·5	37·5	45·0	43·0	—	—	72·0	0·59
27	Cleared	—	1·0	17·0	29·0	36·5	—	—	56·0	0·46

Average elongation-rate, 0·57 cm. per week.

Strip 2. April 1942 to September 1944 (843 days)

Square no.	Av. length of 10 longest plants (cm.)	Rate of growth per week (cm.)
11	65·5	0·53
12	70·0	0·56
13	73·0	0·59
14	78·0	0·63

Average elongation-rate, 0·58 cm. per week.

Strip 3. August 1942 to September 1944 (762 days)

Square no.	Av. length of 10 longest plants (cm.)	Rate of growth per week (cm.)
13	75·5	0·69
14	76·4	0·70
15	71·8	0·65
16	73·1	0·67

Average elongation-rate, 0·68 cm. per week.

TABLE XXIX. GROWTH-RATE OF *FUCUS SERRATUS* BY CLEARED AREA METHOD IN THE ISLE OF MAN

Port St Mary and Castletown

Port St Mary

Square no.	Length of plants (cm.) 1943 12 Apr.	7 Aug.	31 Dec.	1944 17 Apr.	Growth-rate per week (cm.)
1	0	14·0	25·0	34·0	0·64
2	0	15·5	27·0	37·2	0·70
3	0	17·5	31·5	45·0	0·85
4	0	11·0	22·5	31·0	0·58
5	0	10·5	23·5	47·8	0·90

Average elongation-rate, 0·73 cm. per week.

Scarlet Point, Castletown

Square no.	Length of plants (cm.) 1943 13 Apr.	9 Aug.	31 Dec.	1944 18 Apr.	Growth-rate per week (cm.)
1	0	15·0	26·5	39·5	0·74
2	0	17·5	30·5	42·5	0·80
3	0	19·0	32·5	49·0	0·90
4	0	15·5	27·0	39·0	0·74
5	0	17·5	33·5	55·5	1·04

Average elongation-rate, 0·84 cm. per week.

TABLE XXX. GROWTH-RATE OF MARKED PLANTS OF *FUCUS SERRATUS* IN ARGYLL. SERRATUS ROCK

Plant no.	Duration of exp. (days)	Increase in length (cm.)	Increase in no. of dichotomies	Growth-rate per week (cm.)
A1	1041	74·0	10	0·50
2	245	22·5	4	0·64
3	496	68·0	10	0·93
4	308	43·0	4	0·97
5	308	30·5	5	0·69
6	248	26·5	6	0·75
7	248	19·0	3	0·53
8	192	35·0	4	1·27
B1	520	74·0	8	0·99
2	248	32·5	2	0·91
3	248	38·0	7	1·07
4	248	39·0	5	1·10
5	190	30·5	3	1·12
6	248	44·5	5	1·82
7	248	47·0	6	1·32
C1	248	35·0	5	0·98
2	248	32·0	5	0·90
3	248	38·0	6	1·07
4	443	24·5	2	0·38
5	443	47·0	6	0·74
6	248	32·5	5	0·91
7	520	11·5	2	0·15
8	248	31·0	5	0·87

Average elongation-rate, 0·90 cm. per week.

TABLE XXXI. GROWTH-RATE OF *FUCUS SERRATUS* BY CLEARED AREA METHOD IN ARGYLL

Serratus Rock

Square no.	Duration of exp. (days)	Growth-rate per week (cm.)
E 1	315	0·88
E 2	315	1·06
E 3	315	1·08
A 1	385	0·83
A 2	385	0·72
B and C	385	1·10
D	385	0·90
1	982	0·78
2	238	0·91
3	178	0·82

Average elongation-rate for area, 0·91 cm. per week.

Ascophyllum Rock

Square no.	Duration of exp. (days)	Length of plant (cm.)	Growth-rate per week (cm.)
West strip: 3	1031	70·0	0·47
5 and 6	1031	90·0	0·66

Average elongation-rate for area, 0·57 cm. per week.

TABLE XXXII. WEIGHTS OF FUCOID POPULATIONS IN DEVON AND ARGYLL

Experimental area	No. of months of growth	Species present on areas *F.v.*	*F.s.*	*A.*	Wt. in kg. per m.²
Devon. Wembury strip, 3 m. wide					
Square 4:	Original population	−	+	+	15·6
East	36	+	+	−	14·8
Middle	36	+	+	+	14·3
West	36	+	+	+	15·7
Square 8	36	−	+	−	15·6
Square 14:	16	+	+	−	7·9
High level	28	+	+	−	16·0
Low level	28	+	+	−	9·2
Square 15:	Original population	−	+	+	9·1
(*a*)	34	−	+	−	11·5
(*b*)	34	−	+	−	12·3
Square 16	36	−	+	−	22·9
Square 19	Original population	−	+	−	9·7
	28	+	+	−	17·0
Square 19*a*: South	31	−	+	−	20·0
North	31	−	+	−	7·5
Square 21	Original population	−	+	−	12·4
	36	−	+	−	22·2
Square 21*a*	36	−	+	−	9·2
Argyll					
Ascophyllum Rock:					
West strip 1	33	−	+	+	13·0
2	33	+	+	+	4·6
3	33	−	+	+	9·9
4	33	−	+	−	42·4
East strip	33	−	+	−	2·1
Area 3	16	+	+	+	23·3
Serratus Rock:					
1	Original population	−	+	−	13·1
	33	−	+	−	13·3
2	Original population	−	+	−	27·9
	33	−	+	−	25·5
Lobster Pond	Original population	+	−	−	6·8
	27	+	−	+	6·7
Sgeir Bhuidhe	27	+	−	−	6·7

F.v. = *F. vesiculosus; F.s.* = *F. serratus; A.* = *Ascophyllum.*

Table XXXIV. Analysis of Population in Size Groups. Port Erin

Strip. 1. *Fucus vesiculosus* and *Fucus serratus*. Original population

Metre sq. no.	Total no. plants	Under 10 cm.	10–29 cm.	29–59 cm.	Over 59 cm.
1	124	51	43	20	10
2	847	802	28	14	3
3	962	902	30	27	3
4	332	235	50	42	5
5	788	729	37	20	2
6	660	319	301	38	2
7	310	305	5	—	—
8	1166	1154	10	2	—
9	2168	2151	12	5	—
10	421	394	17	8	2
11	393	326	46	15	6
12	243	202	20	18	3
13	597	560	21	14	2
14	907	835	41	25	6
15	957	843	43	59	12
16	876	713	39	86	38
17	904	762	77	45	20
18	1258	801	380	37	40
19	755	665	25	30	35
20	1150	1008	45	63	34
21	433	344	46	29	14
22	636	589	31	16	—
23	720	645	61	14	—
24	381	314	43	24	—
25	14	3	3	8	—
26	27	26	1	—	—
27	47	14	15	18	—
		Strip 2. Original population			
11	68	27	28	12	1
12	12	0	7	3	2
13	3132	3095	19	16	2
14	981	943	38	—	—
15	2977	2945	10	19	3
16	1637	1597	7	26	7
17	4615	4535	14	53	13
		Strip 2. Final population. *F. vesiculosus*			
11	214	183	20	4	7
12	188	41	41	69	37
13	614	518	38	44	14
14	981	943	18	13	7
15	—	—	—	—	—
16	98	64	32	—	—
17	218	177	21	20	—
		Strip 2. Final population. *F. serratus*			
11	125	58	37	24	6
12	305	160	57	77	9
13	481	281	78	103	19
14	700	391	177	106	26
15	626	470	109	47	—
16	1194	750	273	133	38
17	1114	670	249	175	20
		Strip 3. Final population. *F. serratus*			
13	1248	390	423	393	42
14	866	192	320	296	58
15	1110	114	536	414	46
16	1212	536	453	176	47

Table XXXIII. Sequence of Reproductive Stages through the Year in *Fucus*

Size of plants Area I, Dec. 1941 Area II, Dec. 1942 — Occurrence of different stages in receptacle development and mat

Length (cm.)	No. of dichotomies	1942 Mar.	Apr.	June	July	Aug.	Sept.	Oct.	Nov.	1943 Jan.	Feb.	Mar.
9·0	2	S	S	S	S	S	S	S	S	—	1	3, 4
16·0	5	S	S	S	S	S	S	S	S	2	2	—
22·0	6	4	6	6, 7	7, 8	7, 8	8	9, S	9, S	3, 4, 9	2, 4, 9	4, 6, 9
24·0	10	4, 9	5, 9	6, 7, 9	7, 8, 9	8, 9	8, 9	9, S	9, S	Gone	—	—
26·0	6	S	6	6	7, 8	7, 8	8	9, S	9, S	2–4, 9	1, 4, 9	4, 6, 9
34·0	9	5	6, 7	7	8	8	8	9, S	9, S	—	1, 3, 6, 9	4, 6, 9
36·0	9	5, 9	5, 9	6, 7, 9	6–9	8, 9	8, 9	9, S	9, S	1, 4, 9	1, 4, 9	4, 6, 9
44·0	16	5, 9	6, 9	6, 7, 8, 9	7–9	7–9	8, 9	9, S	9, S	3, 4, 9	Gone	—
44·0	18	5, 9	6, 9	7, 9	7–9	—	8, 9	9, S	9, S	2, 3, 9	2, 4, 9	4, 6, 9
46·0	18	5, 9	6, 9	6, 7, 9	6–9	7–9	8, 9	9, S	9, S	—	2, 5, 9	4, 6, 9
48·0	11	5, 9	6, 9	6, 7, 9	7–9	7–9	8, 9	9, S	9, S	3, 4, 9	2, 5, 9	Gone
19·5	4	—	—	—	—	—	—	—	—	S	S	S
19·5	4	—	—	—	—	—	—	—	—	S	S	S
25·0	6	—	—	—	—	—	—	—	—	S	S	S
26·5	7	—	—	—	—	—	—	—	—	1 (few)	2, 3	4
28·0	9	—	—	—	—	—	—	—	—	—	1, 3	4, 6
33·5	11	—	—	—	—	—	—	—	—	S	1	2, 3
34·5	8	—	—	—	—	—	—	—	—	1, 2	1, 3	2, 5
37·0	14	—	—	—	—	—	—	—	—	1 (few)	2, 3, 4	2–5
38·0	13	—	—	—	—	—	—	—	—	1, 3	2, 4	3, 6
38·5	6	—	—	—	—	—	—	—	—	1 (few)	1, 3	2, 6
40·0	14	—	—	—	—	—	—	—	—	1, 3, 9	1–4, 9	3–6, 9
46·0	12	—	—	—	—	—	—	—	—	1, 2	—	3, 6
47·0	14	—	—	—	—	—	—	—	—	1, 2, 9	1, 3, 9	3, 5, 9
49·5	15	—	—	—	—	—	—	—	—	1 (few)	1, 3	1, 6
50·0	15	—	—	—	—	—	—	—	—	1, 2, 9	1, 2, 3, 9	1, 5, 9
59·0	14	—	—	—	—	—	—	—	—	1, 3, 9	—	1, 5, 9
59·0	21	—	—	—	—	—	—	—	—	1, 3, 9	2, 4, 9	2, 6, 9
61·0	19	—	—	—	—	—	—	—	—	1, 2, 9	1, 5, 9	1, 6, 9
66·0	23	—	—	—	—	—	—	—	—	1, 3, 9	2, 3, 9	2, 6, 9
67·0	24	—	—	—	—	—	—	—	—	1, 2, 9	1–4, 9	2, 6, 9
69·0	20	—	—	—	—	—	—	—	—	2, 4, 9	1, 5, 9	2, 6, 9
69·0	31	—	—	—	—	—	—	—	—	2, 4, 9	2, 6, 9	3, 6, 9
71·0	21	—	—	—	—	—	—	—	—	1, 3, 9	1, 5, 9	2–6, 9
71·5	18	—	—	—	—	—	—	—	—	1, 2, 9	2, 4, 9	3–6, 9
73·0	22	—	—	—	—	—	—	—	—	1, 3, 9	1, 4, 9	1, 6, 9
75·0	19	—	—	—	—	—	—	—	—	1, 3, 9	2, 5, 9	3, 6, 9
77·0	25	—	—	—	—	—	—	—	—	2, 4, 9	1, 4, 9	2, 6, 9
82·0	32	—	—	—	—	—	—	—	—	1–4, 9	2–6, 9	2–6, 9
89·0	31	—	—	—	—	—	—	—	—	1, 2, 3, 9	2–4, 9	3, 6, 9
95·0	37	—	—	—	—	—	—	—	—	1, 3, 9	2–4, 9	4, 6, 9
105·0	33	—	—	—	—	—	—	—	—	2, 4, 9	2, 5, 9	1, 6, 9

ULOSUS ON THE DEVON COAST AS SHOWN BY A NUMBER OF INDIVIDUAL PLANTS

Stages 1–9 (see p. 474). S indicates whole plant sterile

May	June	July	Oct.	Nov.	Dec.	1944 Jan.	Mar.	Apr.	May	June	July	Aug.
6	6	7–9	9, S	9, S	9, S	Gone	—	—	—	—	—	—
—	9, S	9, S	9, S	9, S	9, S	9, S	9, S	Gone	—	—	—	—
6–9	6–9	9, S	Gone	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
6–9	6–9	7–9	8, 9	Gone	—	—	—	—	—	—	—	—
7–9	7–9	7–9	9, S	1, 9	9, S	9, S	9, S	9, S	9, S	9, S	9, S	Gone
6, 9	6–9	7–9	8, 9	9, S	1, 9	1, 3, 9	6, 9	Gone	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
4, 6–9	6–9	7–9	9, S	1, 9	, 2, 9	1, 3, 9	Gone	—	—	—	—	—
6, 9	6–9	7–9	9, S	Gone	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
S	S	S	S	1	1, 2	1, 4	2, 5	1, 5	3, 6	6, 8	6–8	6–9
S	S	S	S	1	2, 4	1, 4	1, 5	3, 5	6	6–8	7, 8	8, 9
1(1 tip)	—	6	9, S	1, 9	1, 9	1–5, 9	Gone	—	—	—	—	—
5, 6	8	8	9, S	1, 9	–3, 9	Gone	—	—	—	—	—	—
5, 6	6	7	9, S	1, 2, 9	—	—	3, 4, 9	4, 5, 9	6, 9	6–9	7–9	7–9
4, 6	5, 6	7	9, S	1, 9	2, 9	1, 3, 9	3, 4, 9	1, 4, 9	3, 6, 9	6–9	Gone	—
4, 6	6	6, 7	8, 9	1, 9	1, 9	1, 3, 9	2, 4, 9	1, 5, 9	4, 6, 9	6–9	6–9	Gone
5, 6	6	6–8	8, 9	1, 9	1, 9	1–4, 9	2, 4, 9	1, 5, 9	4, 6, 9	4–6, 9	6–9	6–9
4, 6	3, 4, 6	6–8	9, S	9, S	, 2, 9	1, 2, 9	1, 4, 9	3, 5, 9	1, 5, 9	4, 6, 9	4, 6, 9	6–9
3, 4, 6	6, 7	8	1, 2, 9	1, 3, 9	, 4, 9	1, 6, 9	1, 6, 9	3, 6, 9	6–9	6–9	7–9	7–9
5, 6, 9	5, 6, 9	6, 9	7–9	1, 9	, 2, 9	1, 4, 9	2–5, 9	1, 5, 9	3, 6, 9	6–9	6–9	7–9
5, 6	4, 6	6, 7, 8	8, 9	9, S	, 3, 9	Gone	—	—	—	—	—	—
3, 4, 6, 9	4, 6	6, 7	7–9	1, 9	1, 9	1, 3, 9	2, 4, 9	1, 5, 9	4, 6, 9	6–9	6–9	Gone
4, 6	4, 6	7	9, S	9, S	9, S	Gone	—	—	—	—	—	—
5, 6, 9	3, 4, 6, 9	6, 9	6–9	8, 9	1, 9	1, 3, 9	1, 4, 9	1, 5, 9	4, 5, 6, 9	6–9	6–9	7–9
5, 6, 9	6, 9	6–9	8, 9	1, 9	, 2, 9	1, 3, 9	1, 6, 9	1, 6, 9	3, 6, 9	4–9	6–9	9, S
4, 6, 9	4, 6, 9	9, S	9, S	9, S	9, S	1, 3, 9	2, 9	4, 9	4, 6, 9	7, 9	8, 9	8, 9
5, 6, 9	6, 9	6–9	7–9	1, 9	, 2, 9	1, 4, 9	1, 6, 9	1, 6, 9	3, 6, 9	6, 9	Gone	—
4, 6, 9	4, 6, 9	6–9	Gone	—	—	—	—	—	—	—	—	—
5, 6, 9	6, 9	6–9	Gone	—	—	—	—	—	—	—	—	—
5, 6, 9	6–9	7–9	1, 8, 9	1, 2, 9	, 4, 9	1, 5, 9	2, 6, 9	9, S	9, S	9, S	9, S	9, S
6, 9	3, 6, 9	6–9	6–9	1, 3, 9	1, 3, 9	Gone	—	—	—	—	—	—
5, 6, 9	6, 7, 9	6–9	Gone	—	—	—	—	—	—	—	—	—
4, 6, 9	4, 6, 9	6–9	Gone	—	—	—	—	—	—	—	—	—
5, 6, 9	6, 8, 9	7–9	8, 9	1, 9	1, 2, 9	1, 4, 9	2, 5, 9	1, 5, 9	3, 6, 9	Gone	—	—
3, 4, 6, 9	2, 3, 6–9	3, 4, 9	7–9	1, 9	1, 2, 9	1, 5, 9	3, 6, 9	1, 6, 9	6, 9	6, 7, 9	7–9	9, S
4, 6, 9	6, 9	7–9	8, 9	8, 9	9, S	1, 9	1, 2, 9	1, 4, 9	3, 5, 9	6, 9	6–9	7–9
5, 6, 9	4–9	6–9	6–9	8, 9	1, 9	Gone	—	—	—	—	—	—
5, 6, 9	6, 9	6–9	8, 9	8, 9	9, S	Gone	—	—	—	—	—	—
4, 6, 9	6, 9	Gone	—	—	—	—	—	—	—	—	—	—
4, 6, 9	6, 7, 9	7–9	9, S	9, S	9, S	9, S	9, S	9, S	9, S	9, S	9, S	9, S

ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

The Annelid Phosphagen: With a Note on Phosphagen in Echinodermata and Protochordata

By E. Baldwin and W. H. Yudkin

Proc. Roy. Soc. B, Vol. 136, 1950, pp. 614–31

A new, arginine phosphate-like phosphagen is present in annelid and gephyrean worms.

A second phosphagen, possibly identical with creatine phosphate, has also been found in certain annelids but not so far in gephyreans. This second phosphagen sometimes co-exists with the first, but is found alone in some species.

The distribution of these two phosphagens does not appear to be correlated with physiological activity or with environmental factors.

Arginine could not be isolated from either of two annelid or one gephyrean species; a new base is, however, present in the guanidine fraction and has been isolated as the picrate. It has not yet been identified.

The significance of these observations is discussed in relation to the taxonomic status of the Annelida and Gephyrea. It is indicated that there exists a close relationship between these groups.

The new 'annelid phosphagen' is, apparently, confined to the Annelida and Gephyrea, which are thus chemically distinguishable from the Arthropoda and Mollusca.

Some new data are presented concerning the distribution of arginine and creatine phosphates in Echinodermata and Hemichordata, and the evidence concerning these two groups is reviewed with special reference to the echinoderm-hemichordate theory of vertebrate ancestry.

It is concluded that existing data support this theory, and that the new information concerning the phosphagens of the annelids serves to emphasize the wide divergence that exists between the segmented invertebrates and the true Chordata. E.B.

The Effect of Temperature on the Electrical Activity of the Giant Axon of the Squid

By **A. L. Hodgkin** and **B. Katz**

Journ. Physiol., Vol. 109, 1949, pp. 240–9

The giant nerve fibre of *Loligo* provides excellent material for measurements of the electrical characteristics of the surface membrane. The present paper contains an account of experiments dealing with the effect of temperature on the action potential. It is shown that the absolute magnitude of the action potential decreases with increasing temperature but that the resting potential remains practically constant over the range 0–20° C. The time course of the spike is greatly accelerated by a rise in temperature. The rate of decline of the spike appears to have a higher temperature coefficient than the rate of rise.

A.L.H.

The Effect of Calcium on the Axoplasm of Giant Nerve Fibres

By **A. L. Hodgkin** and **B. Katz**

Journ. Exp. Biol., Vol. 26, pp. 292-4, 1949

It is well known that a rod of axoplasm can be obtained by extruding the contents of a giant nerve fibre, and that if this is done in sea water, the axoplasm disperses rapidly. The present paper contains a brief account of experiments dealing with the effect of ions on this phenomenon. It is shown that dispersal of axoplasm from the giant axon of *Loligo* depends upon the presence of small concentrations of calcium. No dispersal occurs in isotonic calcium-free solutions of sodium or potassium chloride. A.L.H.

The Effect of Sodium Ions on the Electrical Activity of the Giant Axon of the Squid

By **A. L. Hodgkin** and **B. Katz**

Journ. Physiol., Vol. 108, 1949, pp. 37–77

In recent years physiologists at Plymouth and at Woods Hole have made an intensive study of the giant nerve fibre of *Loligo*. One of the most interesting results of this work has been the finding that the action potential of a nerve fibre is associated with a reversal of potential difference across the surface membrane. For some time no satisfactory way of accounting for this effect

could be found, but it now appears that it may have an interesting explanation in terms of permeability and ionic concentration. Chemical studies have shown that potassium is concentrated in the interior of a nerve fibre whereas sodium is relatively dilute. Experiments described in the present paper suggest that the surface membrane is able to alter its ionic permeability in a remarkable manner during activity. In the resting nerve fibre the membrane appears to be more permeable to potassium than to sodium, and this has the effect of making the inside of the nerve fibre negative with respect to the outside. During activity the membrane does not break down, as was formerly supposed, but reverses the resting condition by becoming highly and specifically permeable to sodium. This change allows sodium to enter the nerve fibre faster than potassium can leave it, with the result that the inside of the nerve fibre becomes positive with respect to the outside. This state of affairs must be transitory, and it is suggested that the rise in sodium permeability is short-lived and that the membrane potential is restored to its resting level by an outward migration of potassium ions.

The 'sodium hypothesis' is supported by the following observations: (i) conduction of impulses is impossible in sodium-free media; (ii) the potential difference across the active membrane varies with the external concentration of sodium in the manner predicted by the hypothesis; (iii) the rate of depolarization of the nerve membrane can be varied over a wide range by altering the external concentration of sodium. A.L.H.

Internode Lengths in the Nerves of Fishes

By P. Kynaston Thomas and J. Z. Young

Journ. Anat., Vol. 83, 1949, pp. 336–50

Measurements of internodal distance and diameter were made on isolated nerve fibres dissociated in glycerin after formalin fixation and osmic acid staining. Several marine fishes were investigated, including *Raia clavata*, *Scyliorhinus canicula*, *Torpedo ocellata* and *Conger conger*.

In the lateral line nerves of the ray and conger eel, the distance between the nodes may reach 8 mm. on the largest fibres. In mammals the corresponding value is 1·5 mm. Internode length increases more rapidly with diameter in the lateral line branch of the vagus than in the branchial branches, and more rapidly in the lateral line nerves of larger than of smaller fishes. In lateral line nerves from fishes of different lengths the ratio of the maximum internode length to the length of the animal is approximately constant. There is not, therefore, a fixed internode length for each fibre diameter, the correlation between the variables being due to the fact that both are correlated with growth.

There is a sharply defined minimum internodal distance of about 0·2 mm. in the various fishes studied, and this is also found in other animal groups.

The conditions in fishes and other vertebrates are consistent with the view that internode length is determined when the nodes are first formed, possibly by surface tension, and later by the amount of growth in length of the nerve. When medullation takes place internode length is short, and is the same for all fibres. As growth proceeds, a relationship between internode length and diameter appears, such that the larger fibres have longer and the smaller shorter internodes. There is little change in the number of nodes after medullation; as the nerves elongate so, too, do the internodes. The occurrence of longer internodes on the larger fibres would be explained if the ultimately larger fibres became myelinated earliest. P.K.T.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1949–50

The Council has to record with deep regret the deaths of Prof. Walter Garstang, formerly a member of the Scientific Staff of the Association's laboratories at Plymouth and at Lowestoft, and later a Vice-President and an Honorary Member; Mr R. A. Todd, also an early member of the Scientific Staff contemporary with Prof. Garstang; Prof. August Krogh, For.Mem.R.S., an Honorary Member of the Association; and Dr Robert Gurney, a Founder of the Association.

The Council and Officers

Four ordinary meetings of the Council were held during the year, three in the rooms of the Royal Society, and one at the Plymouth laboratory. At these the average attendance was sixteen. The Association is indebted to the Council of the Royal Society for the use of their rooms, and to the Council of the Linnean Society for the use of their rooms for the Annual General Meeting.

During the year Dr J. E. Smith was appointed as Governor representing Cambridge University in place of Dr C. F. A. Pantin, F.R.S.; and Mr Harrison S. Edwards representing the Fishmongers' Company in place of Mr A. R. Wagg.

The Plymouth Laboratory

All the major war damage repair and rebuilding having now been completed, attention has been devoted to the equipment of the buildings with furnishings and fittings.

A 15-in. Colchester lathe and tools for sheet metal work have been installed in the workshop; an additional electric power line has been laid. An old doorway in the passage connecting the north and south buildings has been renewed and opened up to give easy access to the main workshop.

The full equipment of both the main workshop and the physiology workshop has added greatly to the scope of the work of the laboratory, enabling the development of many new types of apparatus for research at sea.

The Aquarium

The aquarium has proved as popular as ever, particularly with summer visitors, and many parties of school children have attended with their teachers. The stock of fishes and invertebrates in the tanks has been maintained at capacity.

The display has been much improved by the addition of a number of

coloured drawings illustrating the animals in the tanks. These have been painted by students of the Plymouth City School of Art, and thanks are due to the Principal, Mr L. Duckett, M.C., A.R.C.A., and to the students themselves, especially Miss Jenefer Peter and Mr H. Williams.

Dr D. P. Wilson has recorded in Vol. XXVIII, No. 2, of the *Journal* some observations on the lives and habits of a variety of species living in the aquarium. Among these is the record of a *Sabella* which has lived in one of the tanks for over ten years.

Research Ships

The research vessels *Sabella* and *Sula* have worked regularly throughout the year. As reported last year, the *Sula* has proved to be a most efficient and useful little ship and has made it possible for the *Sabella* to undertake extended cruises to more distant waters both up and down Channel.

By the beginning of this year deterioration of the underwater metal sheathing of the *Sabella* had reached a point where it became necessary either to remove it altogether or to make extensive renewals of the metal. By permission of the Admiralty the sheathing has been removed. To carry out this work *Sabella* was placed in dry dock during the first fortnight in June.

All the necessary requirements having now been completed the *Sula* has been accepted for classification by Lloyds.

The motor-boat *Gammarus* has, as usual, worked regularly throughout the year, apart from brief periods for normal maintenance of hull and engines.

In December 1948 permission was obtained from H.M. Treasury to incur costs necessary for the preparation of plans and specifications for a proposed new research vessel to replace *Sabella*. In co-operation with Messrs Graham and Woolnough, a Liverpool firm of Naval Architects, these have been completed and have formed the basis of tenders from selected firms for the construction of the vessel.

The Staff

Mr N. A. Holme was appointed to the staff in the grade of Scientific Officer in April 1949.

Dr J. A. C. Nicol was appointed to the staff in the grade of Senior Scientific Officer in June 1949.

Dr J. S. Alexandrowicz was appointed to the staff in the grade of Temporary Senior Scientific Officer on 1 January 1950.

Mr D. K. Hill resigned from the post of Physiologist on the staff on 30 September 1949, to take up an appointment to direct a new Department of Biophysics at the British Post-graduate Medical School at Hammersmith.

Mr F. S. Russell, Dr H. W. Harvey and Mr P. G. Corbin attended the thirty-seventh meeting of the International Council for the Exploration of the Sea in Edinburgh in October 1949.

Occupation of Tables

The following one hundred and nine workers have occupied tables at the Plymouth laboratory during the year:

B. C. Abbott, London (Physiology of dogfish muscle).
Miss E. B. Albrecht, London (Behaviour of *Arenicola ecaudata*).
Dr A. A. Aleem, London and Alexandria (Littoral diatoms).
Dr X. M. Aubert, London and Louvain (Physiology of dogfish muscle).
T. Bagenal, Cambridge (Identification of fishes).
R. Bainbridge, Oxford (Plankton interrelationships).
Dr Elizabeth J. Batham, Cambridge (Nerve net of sea anemones).
A. C. G. Best, London (Histology of marine animals).
G. Bolster, Oxford (General zoology).
Dr Anna M. Bidder, Cambridge (Library).
Dr Hans Borei, Stockholm (General).
Dr P. Buffa, Oxford (Effects of sodium fluoracetate on marine animals).
Miss E. M. Brown, London (Parasitic Dinoflagellates).
B. C. Browne, Cambridge (Geology and geophysics of ocean bed).
Prof. S. F. Bush, Natal (Laboratory organization).
H. W. Chang, Academia Sinica, Shanghai (Biology of *Callionymus*).
Dr G. Chapman, London (Mesogloea of *Calliactis*).
Dr P. N. J. Chipperfield, I.C.I., Brixham (Library).
K. U. Clarke, London (General zoology).
Miss E. Clay, I.C.I., Brixham (Algal cultures).
Dr & Mrs N. E. Collias, Wisconsin (Littoral fauna).
F. R. Coombe, Plymouth (Physical properties of sand grains).
R. A. Cox, National Institute of Oceanography (Oceanographical methods).
Dr D. J. Crisp, I.C.I., Brixham (Library).
Dr D. R. Crofts, London (Mollusc embryology).
R. I. Currie, National Institute of Oceanography (Chemistry of sea water).
Prof. J. F. Danielli, London (Nucleus transplantation in *Echinus* eggs).
E. J. Denton, Aberdeen (Nerve fibres in *Carcinus*).
Miss E. Dresel, Cambridge (Excretion in Isopods and Amphipods).
J. E. Elgood, London (General zoology).
D. Etherington, London (Sporozoan parasite in *Phascolosoma minutum*).
G. R. Fish, Colonial Office (Culture of phytoplankton).
J. E. Forrest, London (Nudibranchs).
G. R. Forster, D.S.I.R. (Biology of prawns).
H. C. Fountain, Torpoint (Marine Acarines).
Dr Vera Fretter, London (Ecology and structure of *Cerithiopsis* and *Triphora*).
T. Gascoyne, London (Biology of *Tritonia*).
Prof. J. Gray, F.R.S., Cambridge (Locomotion of fishes).
Miss U. M. Grigg, D.S.I.R. (Biology of Trochids).
Surg. Lieut. D. O. Haines, R.N., H.M.S. *Challenger* (General).
Dr J. E. Hale, London (Chlorocruorin haem in *Sabella*).
R. E. Hall, Southampton (Marine Chironomids).
R. Hamond, Holt, Norfolk (Hydroids and Polyzoans).
Dr J. P. Harding, British Museum (Nat. Hist.) (Colour photography of Entomostraca).
Miss M. B. Harley, Durham (Feeding in *Nereis diversicolor*).
Dr T. J. Hart, National Institute of Oceanography (Ice diatoms; hake).

M. N. Hill, Cambridge (Geology and geophysics of ocean bed).
A. L. Hodgkin, F.R.S., Cambridge (Neurophysiology).
Prof. Sven Hörstadius, Uppsala (Nucleus transplantation in *Echinus* eggs).
W. R. Howells, Aberystwyth (Intertidal ecology).
O. D. Hunt, Newton Ferrers (Fouling organisms).
Prof. E. G. Hutchinson, Yale (Mineral inclusions in marine animals).
A. F. Huxley, Cambridge (Neurophysiology).
P. H. Jellinek, Cambridge (Marine ecology).
Dr M. W. Jepps, Glasgow (Life history of *Polystomella*).
R. Johnston, Aberdeen (Chemistry of sea water).
F. R. Harden Jones, Colonial Office, (General; swim bladder in fishes).
W. C. Jones, Cambridge (Orientation of sponge spicules).
K. A. Joysey, London (Echinoderms).
Dr B. Katz, London (Neurophysiology).
Dr G. Y. Kennedy, Sheffield (Pigments of *Branchiomma* and *Aplysia*).
R. D. Keynes, Cambridge (Neurophysiology).
Prof. W. B. R. King, F.R.S., Cambridge (Geology and geophysics of ocean bed.)
Dr F. G. W. Knowles, Marlborough College (Control of pigment movement in Crustaceans).
Miss P. Kott, Australia (Colonial Tunicates).
G. Krishnan, Manchester (Physiology of sinus gland in crabs).
Dr Marie V. Lebour, Cawsand (Decapod Crustaceans).
Dr P. R. Lewis, Cambridge (Neurophysiology).
Dr H. W. Lissman, Cambridge (Locomotion of fishes).
Dr Joan I. Lorch, London (Nucleus transplantation in *Echinus* eggs).
Dr A. G. Lowndes (Entomostraca).
Dr Sidnie M. Manton, F.R.S., London (Locomotion of Arthropods and Polychaetes).
Dr L. Harrison Matthews, Bristol (Locomotion of fishes).
M. D. Menon, Madras (Biology of *Gadus luscus* and *G. minutus*).
M. N. Mistakidis, Conway (Library).
Miss V. Moyle, Cambridge (Excretion in Isopods and Amphipods).
Prof. Lily Newton, Aberystwyth (Library).
V. Novak, Cambridge (Sinus gland hormones of Crustaceans).
Dr T. Ouang, Amoy (Hatching gland of dogfish embryo).
Dr C. F. A. Pantin, F.R.S., Cambridge (Nerve net of sea anemones).
Prof. R. A. Peters, F.R.S., Oxford (Effect of sodium fluoracetate on marine animals).
W. T. W. Potts, Cambridge (Microanalytical methods for inorganic ions).
Dr R. D. Purchon, Cardiff (Rock-boring Lamellibranchs).
Dr Jeanette L. Rayment, Edinburgh (Radioactive tracers and algae).
Dr. T. D. M. Roberts, Glasgow (Electrophysiology of Cephalopod eye).
Dr J. D. Robertson, Glasgow (Microanalysis of inorganic ions in *Sepia*).
G. A. Robinson, Development Commission (Phytoplankton).
M. Roessingh, Leiden (Plankton).
Dr E. S. Russell, Hastings (Decapod Crustaceans).
Dr L. Silén, Stockholm (Biology of Polyzoans. Fixation of *Phoronis*).
Dr E. W. Simon, Oxford (Toxicity studies in *Echinus* eggs).
B. W. Sparrow, Newton Ferrers (Fouling organisms).
Miss F. A. Stanbury, Plymouth (Library).
Miss M. F. Sutton, London (Regeneration in *Ciona*).
J. Swallow, Cambridge (Geology and geophysics of ocean bed).
R. V. Tait, London (General).

Prof. R. V. Talice, Uruguay (General).
A. G. Taylor, Freetown (General).
Dr Harold Thompson, Australia (General).
D. Vaux, Lowestoft (Physical oceanography).
P. R. Walne, Conway (Chemistry of sea water).
I. M. Watt, Exeter (Underwater photography).
Dr J. E. Webb, Nigeria (General zoology).
Dr G. Weddell, Oxford (Staining of corneal nerve fibres).
Dr S. Weidmann, Berne (Neurophysiology).
G. P. Wells, London (Behaviour of *Arenicola ecaudata*).
Dr E. Westblad, Stockholm (Turbellarians).
Dr W. H. Yudkin, Cambridge (Phosphagens in Polychaetes).
Dr E. Zander, Oxford (Staining of corneal nerve fibres).

A very large number of short visits have been made by research workers wishing to see the work of the laboratory or to discuss their problems with individual members of the staff. Among these the following have come from overseas: Dr Nazir Ahmad, E. Pakistan; Miss L. M. Angel, Adelaide; H. C. Aslyng, Denmark; Prof. and Mrs G. P. Baerends, Groningen; R. Bassindale, Achimota College, Gold Coast; Prof. and Mrs L. R. Blinks, Pacific Grove; Señora Bonilla, Uruguay; D. F. Bumpus, Woods Hole; Dr C. Lalor Burdick, New York; Dr B. Kullenberg, Göteborg; Miss D. F. McCarthy, Adelaide; Dr M. F. E. Nicolai, Leiden; Dr K-G. Nyholm, Uppsala; Prof. T. Park, Chicago; Dr W. Rodhe, Uppsala; W. F. Royce, Woods Hole; E. F. Scott, New Zealand; Miss N. G. Sproston, Shanghai; Dr E. A. Thomas, Zurich; E. C. Zimmerman, Honolulu; J. Pericot and J. Baca, Barcelona.

The Easter Vacation Courses were conducted by Mr G. M. Spooner and Mr P. G. Corbin, and were attended by forty-five students from the following Universities and University Colleges: Oxford, Cambridge, Glasgow, Aberdeen, Dublin, Durham, London, Sheffield, Cardiff, Exeter, Hull, Leicester, Southampton, and from Chelsea Polytechnic, Middlesex Hospital, and Plymouth Technical College.

Also during the Easter Vacation Mr P. H. F. White brought nine boys from Harrow School, and Miss M. E. Morris five from the Bec School, London.

Scientific Work of the Plymouth Laboratory Staff

With the increasing number of visiting workers, and especially of younger scientists preparing for posts at home and abroad, much of the time of the scientific staff has inevitably been taken up in giving help and advice. This is an important side of the work of the laboratory which is contributing to the efficiency of the post-war expansion in marine biological investigations.

Physics and Chemistry of Sea Water

Last year's report described in some detail the work on the measurement of daylight in air and under water which is being carried out by Dr W. R. G.

Atkins in collaboration with Dr H. H. Poole, Mr F. J. Warren and Miss P. G. Jenkins. This work has been continued and is being prepared for publication. Special attention has been given to the re-standardization of photocells and to the examination of new ones. The determination of the vertical extinction coefficient of natural waters by the photoelectric balance by depth seems to be a simple method which is scarcely affected by sudden fluctuations in the intensity of daylight. Dr Atkins worked with Dr Poole in the Royal Dublin Society's laboratory during parts of May and June.

Much time has been devoted to the study of the scattering of light in the Tyndall beam, using the R.C.A. electron multiplier cell, the sensitivity of which is vastly greater than that of any cell previously available for use, even with high amplification. Attempts are being made to ascertain the effects due to the different sized particles suspended in the water.

Dr Atkins also continued work on the copper cycle in the sea. The new plastic-lined closing water-bottle made it possible to deal with other than surface samples. As with several other minor constituents the deeper layers are less rapidly depleted than the surface.

Optical methods for the study of suspended matter are being supplemented by chemical analyses and the deposits, algal and inorganic, have been further examined by Dr Atkins and Mr F. A. J. Armstrong.

Dr H. W. Harvey has continued, in collaboration with Mr Armstrong, an investigation of the phosphate and total phosphorus in the waters off Plymouth. The results of this survey, commenced in 1947, will shortly be published. It is thought that this study of the phosphorus cycle in the sea has allowed the water masses passing through the area to be distinguished the one from the other, simply, and at any time of year, in terms of their potential fertility. There is evidence indicating that this potential is rather closely related to the actual productivity of the water mass and to the survival of young fish. This study required some knowledge of the quantity of plants and of pelagic and benthic animals in the area. From information supplied by colleagues and friends and from observations on plant population made during the past year, Dr Harvey has been able to arrive at rough tentative estimates of the average population density of the main ecological groups, and of their food requirements. Since these estimates and their interrelations are of wider interest than that for which they were originally made, an account will be published in the *Journal*.

Dr L. H. N. Cooper has continued to re-assess and correlate earlier work in the English Channel, Celtic Sea and the adjacent waters of the Atlantic Ocean. In collaboration with Mr David Vaux he has dissected one thread from the pattern of events, the effects of winter cooling of the water south-west of Ireland. In some winters this may become heavier than the adjacent oceanic surface water. It then tends to flow westward over the shelf to the edge of the slope where it may sink until it meets water of similar density. In this way shelf water may be carried down to a depth of 600 m. or more. This

'cascaded' water may be recognized by its high oxygen content. The results have been published in Vol. XXVIII, No. 3, of the *Journal*, together with further developments and applications to the hydrography of the Celtic Sea.

Amongst the hydrographical records obtained south-west of Ireland between 1910 and 1913 by the Irish Fisheries Service, there were a number which suggested that heavy water overlaid lighter. Often these anomalous records were internally consistent so that it seems very doubtful whether they should be dismissed as due to errors of observations. If they are accepted as correct and indicating a density inversion, it becomes possible to follow for 90 miles along the side of the continental slope water which had flowed from the Celtic Sea as a winter cascade. The course of this water is predicted by applying Rossby's wake stream theory to the oceanic water lying off the slope. It would seem likely that Rossby's theory may be widely applied in the Atlantic Ocean south-west of the British Isles and will provide a valuable working hypothesis for unravelling the complex water movements which occur.

Dr Athelstan Spilhaus has observed density inversions in the neighbourhood of the New England continental slope, although the operative causes may there be different. Dr Cooper is maintaining close contact with Dr Spilhaus.

Mr F. A. J. Armstrong has continued the monthly hydrographic cruises to the Station E 1, ten miles beyond the Eddystone, and has carried on the routine phosphate estimations begun by Dr Atkins in 1923. He has also been engaged on improving existing methods of analysis of nitrate, and has applied Dr Harvey's absorptiometer for the estimation of iron with 2:2′-dipyridyl. Experiments are being made to test whether storage of sea water in glass vessels leads to leaching of iron from the walls and precipitation of ferric hydroxide.

Mr Armstrong has collaborated with Dr Harvey in work on the phosphorus cycle, making many analyses of total phosphorus. A short paper by him on corrections in the method for phosphate determination and reproducibility of results has been published in Vol. XXVIII, No. 3, of the *Journal*.

Plankton

Mr F. S. Russell has completed his monograph on the Medusae of the British Isles and the manuscript and the many coloured plates and line drawings have now gone to the Cambridge University Press for printing.

The weekly half-hour oblique hauls with the 2 m. stramin ring-trawl have been continued during the year. Preliminary inspection of the catches by Mr P. G. Corbin shows no marked change from the very low level of production of young fish observed in 1948.

A study of the small coloured flagellate and non-motile forms present in the sea water off Plymouth has been started by Dr Mary Parke. The first stage in the work, now in progress, is the study of the different marine types to be found in these waters so that in any later quantitative work a quick recogni-

tion and classification of single individuals can be made. This study of the different types is being done by the cultivation of the organisms present in samples of sea water taken at intervals during the year. The observations that have been made during the last year for inshore waters suggest that, although most classes are represented throughout the year, there is a rise and fall in the numbers of some classes with the time of the year; for example, the flagellate forms belonging to the Chrysophyceae are most abundant from November to May, while those belonging to the Cryptophyceae (mainly with red pigment) are most common from June to October. In addition to many mixed cultures of these new organisms twenty-five pure cultures of new organisms, started from clones, have been obtained. These cultures include representatives from the following classes: Chlorophyceae, Chrysophyceae, Bacillariophyceae, Cryptophyceae, Dinophyceae, Euglenineae, Myxophyceae and possibly Xanthophyceae.

The stock cultures of marine diatoms and flagellates have been maintained throughout the year, and subcultures have been sent to other institutions for research and teaching purposes.

Arising from the studies on the relation between the phosphorus available in the water and the animal populations, Dr H. W. Harvey is investigating the accuracy of sampling of zooplankton in water of moderate depth by means of vertical net hauls. Meters have been constructed which register the flow of water past them. Provided the ratio of the filtering area of the net to the size of its mouth exceeded a limiting value, substantially the same flow of water was registered when the net was hauled through the same distance of water, irrespective of the position of the meter in the mouth. This allows the use of these meters for measuring the quantity of water filtered by a net. It has been found that a conical net acts as an aerofoil, causing a negative pressure in its wake which assists the passage of water through the net.

A meter, fitted with a device to stop the vanes revolving when the net is lifted from the water, has been supplied to the Fisheries Laboratory at Lowestoft, and has now been in frequent use in a Hensen net for several months. A similar meter has been supplied to the Scottish Fishery Board.

Observations have been made with nets of different sizes and types to determine the nature or degree of patchiness of zooplankton. The aim is to arrive at the simplest means of obtaining a sample truly representative of an area. The workshop facilities have made possible this development of apparatus for a special purpose.

Fauna and Flora of the Sea Floor

Dr D. P. Wilson's experiments on the settlement reactions of *Ophelia bicornis* larvae were continued during the summer-breeding season. Taking, as a starting-point, the result of a single test in 1948 which was not readily interpreted on the assumption that physical size and shape of the sand grains

is the only factor in promoting metamorphosis, a set of experiments was devised which have shown that there is at least one other factor involved, and one which may have an even greater influence. Sand from the nearby Salthouse Lake re-graded to resemble the natural Bullhill sand, in which the adult worms live, repels the larvae more strongly than the slightly greater angularity and roughness of the grains would appear to merit. It was found that when this sand is sprinkled into water in a dried condition most of it will float, whereas the Bullhill sand sample used in the experiments, when similarly treated, almost all sinks. The Salthouse Lake sand becomes readily wettable, and therefore sinkable, after heating to a high temperature; larvae will then settle in it and metamorphose. Extraction of the sand by ether, alcohol or acetone did not destroy its flotability and neither did treatment with aqua-regia; the sand was not made any more attractive to the larvae by the use of these reagents. Contact with finely powdered activated charcoal reduced the flotability of Salthouse Lake sand, but not completely as did heating. The larvae, nevertheless, settled very readily in the sand after this treatment, and a big proportion at once proceeded to metamorphose. Treatment of Bullhill sand with activated charcoal increased its attraction and speeded the onset of metamorphosis. Activated charcoal treatment did not, however, induce larvae to metamorphose in a calcareous sand of similar grade to the quartz sand of the Bullhill Bank. Experiments with the smallest sizes of sand grains after treatment with activated charcoal indicate that size can still be regarded as an important factor in influencing settlement. Work is still in progress and no definite conclusions from this year's results have yet been drawn.

During the year Dr Wilson has published in Vol. XXVIII, No. 2, of the *Journal* an account of the decline of *Zostera* at Salcombe and its effects on the shore. A comparison of old and recent photographs of the eastern shore of the harbour, taken at comparable states of the tide, indicate that at the lower levels the shore has been lowered 2 or 3 ft. as a result of the washing away of sand formerly bound by the roots and rhizomes of the *Zostera*. At the same time, sand has been piling up at high-water mark; some of this must have come from the old *Zostera* beds, but more has accumulated from farther afield.

The fauna near low-water mark is changing in character; it is not as rich as it used to be, particularly in those commensal species for which the Salcombe *Zostera* beds were notable.

Dr Mary Parke is collecting together the data for the second paper on the British Laminariaceae dealing with *Laminaria digitata* (L.) Lamour. So far most of the calculations for the growth of the frond have been made but they have not yet been analysed.

Additions have been made to the collection of preserved specimens of marine algae being built up at the laboratory; the most interesting of these are the very rare algae *Atractophora hypnoides* Crn. and *Gigartina teedii* Lamour., which are new records from the Plymouth area, and *Mesogloia lanosa* Crn. and

Myriocladia loveni J. Ag.? which have not previously been recorded for the Devon coast. The *Myriocladia* may have to be placed in a new species. Further information has been accumulated on the occurrence, distribution and reproduction of the marine algae of the Plymouth area.

Mr G. M. Spooner has continued his work on *Gammarus* and other Amphipoda, and a paper on the occurrence of *G. zaddachi oceanicus* is in preparation. Examination of collections of Amphipoda in general from Plymouth and elsewhere shows how imperfect our knowledge still is of even the species present. *Stenothoë valida* and *Apherusa henneguyi* are new records for the Plymouth area and for Britain. The latter appears to be well established on offshore grounds and to be regularly eaten by *Gadus minutus*. Unrecognized species of *Stenothoë*, *Leucothoë*, *Ampelisca* and *Monoculodes* have also been observed.

In September 1949, Mr Spooner, assisted by Mr N. A. Holme, made a preliminary survey of the fauna of the Helford estuary.

Dr H. G. Vevers has continued his work on the breeding biology of the Plymouth echinoderms. The occurrence in the gonads of *Asterias rubens* of the parasitic ciliate, *Orchitophrya stellarum*, suggests that only rich and well-fed starfish populations are attacked. The parasite has been found in starfishes south of the Eddystone and also in Plymouth Sound, but not in the intermediate Rame-Eddystone Grounds. An attempt is now being made to estimate the density of starfishes and other epifaunal invertebrates by means of photographs taken underwater with an apparatus developed in the laboratory. Photographs have already been taken at depths down to 70 m., but their quality is not yet wholly satisfactory and modifications are being made which should give better definition. The apparatus takes a series of forty to forty-five photographs at each descent, the area covered by each photograph being 1 m. square. A number of such series have now been taken on sand, muddy sand and gravel bottoms near Plymouth. They show a high density of the ophiuroid, *Ophiothrix fragilis*, with smaller numbers of *Asterias rubens* and other echinoderms as well as *Chlamys opercularis*, polyzoan colonies and worm casts. At the depths worked the natural light is quite insufficient to allow an adequate exposure and all lighting is, therefore, done by photofloods worked from the electric mains of R.V. *Sabella*.

Mr N. A. Holme has been continuing his work on techniques for quantitative investigation of the bottom fauna. Using the new bottom sampler, described in Vol. XXVIII, No. 2, of the *Journal*, two series of twenty hauls have been made in Bigbury Bay and Whitsand Bay, with the object of determining the number of samples necessary for a fairly accurate determination of the biomass.

In addition a new type of core sampler is being tested in which the coring tube is made to penetrate more deeply by producing a suction at the top of the tube. The suction is provided by opening a chamber of air at atmospheric pressure under water, the chamber being attached to the top of the coring tube. With this apparatus it is hoped to take cores of 1/50 m.^{2} area and of 30 cm.

depth. Observations on land indicate that suction greatly increases the penetration of a coring tube into sand, but preliminary experiments at sea have not produced cores longer than 15 cm. This may be due to a number of causes, among which is the suggestion, supported by results obtained by Mr M. N. Hill with a free-falling core sampler, that the depth of sand overlying rock in the Plymouth area is less than 30 cm. in many places. It is also possible that the apparatus is not sufficiently weighted, since the buoyancy of the air chamber seriously diminishes its weight under water.

A considerable amount of data has now been collected on the ecology and systematics of the genus *Ensis*. There appear to be three British species: *E. ensis* (L.), *E. siliqua* (L.) and *E. arcuatus* Jeffreys. Examination of named specimens from various collections, however, has revealed the considerable difficulty experienced in identification, particularly in regard to *E. arcuatus* (Jeffreys). The three species inhabit different types of soil: *E. ensis* occurs in fine gravel, *E. siliqua* in clean sand, and *E. arcuatus* in muddy sand. The latter is the least common and most localized of the three species.

Physiology of Marine Organisms

Mr D. K. Hill, who left the staff in October 1949, has continued work with the 200 μ nerve fibre of *Sepia*. The statement made in the last Report, to the effect that it is possible to measure a small increase in diameter of the fibre as the result of stimulation, has been substantiated. This amounts to about 0·2 μ increase in diameter for 10,000 impulses. It appears, however, that the effect is not—as was previously stated—largely due to the difference in volume between the hydrated sodium and potassium ions which are known to exchange across the membrane during activity. It now seems more likely that only about 6 % of the change can be accounted for in this way, and the greater part of the swelling is probably due to an increase in the osmotic pressure of the interior of the fibre brought about by the entry of equivalent amounts of sodium and chloride ions. There is evidence that the fibre undergoes a very small *decrease* in volume initially. This shows up at the start of a period of high-frequency stimulation, but after a few seconds the main phase of swelling supervenes. The maximum shrinkage is about 0·02 μ in diameter. It is only possible to speculate on the cause of this phenomenon.

The kinetics of the penetration of water into the giant fibres of *Loligo* and *Sepia* in response to a change in the external osmotic pressure have been investigated: the results were needed in connexion with the work described above. It was found that the length of a nerve fibre changes when it swells or shrinks: the tension determines which way it goes. When the fibre is under low tension swelling gives an increase in length; if the fibre is put under higher tension the length decreases. In the work on the kinetics of water penetration this change of length was used to follow the volume change; it is a much more sensitive indicator than is the diameter of the fibre.

Work has been continued in connexion with the change in the opacity to white light of a crustacean nerve trunk which is brought about by repetitive stimulation. It was found that the opacity is very sensitive to changes in fibre diameter which follow alterations in the osmotic pressure of the external solution. The response to stimulation is of the right order of magnitude to be attributable to changes in fibre diameter.

Dr J. A. C. Nicol has continued his studies of the nervous system of polychaetes with the intention of concentrating on sensory mechanisms in marine animals. An investigation of photosensitivity in the sabellid *Branchiomma vesiculosum* is now in progress. This has been made possible through the co-operation of Dr Atkins and Mr Warren who have assisted with photoelectric apparatus and measurements. By using the giant axon reflex of *Branchiomma* as an indicator of responsiveness, information has been collected on the sensitivity to changes in light intensity. There is considerable individual variation, but by studying groups of individuals it has been possible to gather statistical data for representative populations. The animals can detect very small decrements in intensity. A relatively greater intensity change is required to evoke a response at low initial intensities than at higher intensities. The animals respond to intensity changes throughout the visual spectrum but appear to be less sensitive to longer wave-lengths. In addition to responding to sudden decreases in intensity, the animals also react to a moving intensity change (i.e. progression of a shadow) across the visual field. Sensitivity to a moving stimulus is much higher than to sudden and uniform decreases in light intensity, and adaptation to the latter does not affect response to a moving stimulus. Various lines of evidence indicate that adaptation occurs neither on the efferent nor on the afferent sides of the reflex pathway, but takes place rather in central correlation areas. *Branchiomma* is unique among non-arthropods in the possession of a primitive form of compound eye. The separate parts of this eye probably facilitate detection of movements.

Dr J. S. Alexandrowicz has continued researches, interrupted by the war, on the nervous system of invertebrates, with special attention to the peculiar innervation of some muscle fibres in Crustaceans. By means of methylene-blue staining these were more closely examined in *Homarus vulgaris* and *Palinurus vulgaris*, and it was found that in the dorsal part of the abdomen there are ganglion cells, four in each segment, which send numerous short richly ramifying processes to the muscles and a long process, one from each cell, to the abdominal ganglionic chain. The muscle bundles in which the short processes terminate show a certain independence and a somewhat different structure from the neighbouring muscles, while the nerve fibres ending in them, besides the cell-processes mentioned above, seem to be also independent in their peripheral course from other nerves running to the muscles. Several ganglion cells of the same kind were also found in the thoracic region.

In the Gastropod *Aplysia punctata* the nerves of the digestive organs were investigated by means of methylene-blue staining. A rich nervous plexus could be seen in the oesophagus, stomach and intestine with a different arrangement of the nervous elements in each of these parts. Nerve cells of various shapes have been found; the bipolar cells, which may be regarded as sensory elements, send one process towards the lumen of the alimentary canal and the other from the opposite side into the nerve-plexus; other cells of unipolar and multipolar appearance and of various sizes are scattered in the walls of the digestive organs or form small groups. In the region where the oesophagus joins the gizzard the nervous elements are arranged in the form of an irregular ring and the ganglion cells are especially abundant at this place.

The results of some exploratory tracer experiments with seaweeds by Mr G. M. Spooner have been published in Vol. XXVIII, No. 3, of the *Journal*. These concern the uptake of the elements strontium and yttrium.

Radioactive strontium is extracted from sea water by the brown seaweeds, in particular by *Fucus serratus*. It is held that this effect is simply a result of ionic exchange, and that the algae regularly contain many times as much strontium in their cell fluids as exists in sea water. On the ionic exchange hypothesis, it appears that *F. serratus* has about 40 times as much strontium as sea water, *F. vesiculosus* about 30, *Ascophyllum nodosum* about 20, and *Laminaria digitata* about 14. By contrast, red algae and green algae such as *Ulva* extract 'active' strontium only to a small or negligible extent. On the above hypothesis, in *Gigartina* the strontium is concentrated by a factor of about 2, while in *Rhodymenia* it may be less than in the sea.

Radioactive yttrium is heavily taken up by the red algae (*Rhodymenia*, *Gigartina*, *Chondrus*) and by the green alga *Ulva*, even to the extent of depleting the water of this element, or very nearly so. The yttrium, however, is not usually heavily taken up by the brown algae, and may, as with a sample of *Fucus vesiculosus* var. *evesiculosus*, be taken up only to quite a small degree.

The diatom *Nitzschia* takes up 'active' yttrium very heavily.

The extraction of yttrium appears to be a matter partly of ionic exchange and partly of *adsorption* on surfaces. It is suggested that both processes may be important with red algae, the former primarily with brown algae, and the latter primarily with *Nitzschia*.

From the 'decay' characteristics of mounted pieces of frond of the red algae and *Ulva*, estimates of the true half-life of Y^{90} were made. The value derived is 63·4 hr. (or 2·642 days).

Fish and Fisheries

During the year Mr G. A. Steven completed a report on the mackerel fishery in the south-west of England with special reference to spawning, feeding and 'fishermen's signs'. This report has been published in Vol. XXVIII, No. 3, of the *Journal*. In last year's Report the importance of 'yellow water'

was mentioned. Further study of mackerel catches from waters of different kinds has provided what appears to be a simple and straightforward explanation of Allen's generalization that the catches of mackerel in May in the Newlyn deep sea fishery are to some extent affected by the amount of sunshine in the same region in February and March.

Data bearing upon the difficult problem of age and growth rate in mackerel are now being worked up. It is found that the otoliths, if carefully cleaned and examined by direct illumination under water against a black background, can be read, though not always with ease even in the younger fish and often not at all in older fish. Age determination by scale readings is also possible, but the scales are so small that the difficulty of obtaining uncontaminated scale samples from large numbers of fish is almost unsurmountable. An additional difficulty is that only a very small proportion of the scales show recognizable growth markings. Nevertheless, a sufficient number has been collected to show that they give readings in agreement with those of the otoliths. The use of otoliths has therefore been adopted as being less tedious and more satisfactory than scales. No skeletal structure has been found that carries reliable indications of annual growth increments.

Because of the difficulty of reading and interpretation in both scales and otoliths much doubt has surrounded the growth and age of mackerel. In 1914, Nilsson published the following figures relating to their growth in Swedish waters:

Length at end of	cm.
1st year	Up to 21·0
2nd year	21·5–28·0
3rd year	28·5–31·0
4th year	31·5–33·0
5th year	33·5–35·0

By contrast, Le Gall, in 1938, gives the following figures for mackerel in the English Channel and Celtic Sea:

Length at end of	cm.
1st year	8–11
2nd year	18–21
3rd year	26–28
4th year	30–32
5th year	About 35

The wide divergence between the results of those two workers for fishes of the two younger year-classes cannot be attributed to differences in locality, especially as preliminary results derived from data collected in 1936 and 1937 in the English Channel and Celtic Sea provided results in agreement with those of Nilsson. Those tentative sizes published in 1939 were:

Length at end of	Up to about
2nd year	27·0 cm.
3rd year	31·5 cm.
4th year	33·5 cm.
5th year	35·0 cm.

Data concerning the length of 1-year-old fish had not then been fully analysed. Further data for the years 1938, 1939, 1940, 1948 and 1949 are now being worked up. The results so far obtained confirm the previous observations and are still in agreement with those of Nilsson, a length of well over 20 cm. often being reached by the end of the first year of life. A report on this work is now being prepared.

Mr P. G. Corbin has continued work on the Ammodytidae. Considerable numbers of the smooth sand-eel, *Gymnammodytes semisquamatus* (recorded as *Ammodytes circerellus* in the Reports of Council for 1947–48 and 1948–49), have been caught in the Plymouth area. It has thus been possible to compare the vertebral numbers of the Plymouth population with that of specimens from Scottish waters. Further comparison of this species with samples of the Mediterranean smooth sand-eel, *G. cicerelus*, and the South African species *G. capensis*, is the subject of a note for the *Journal*. The distribution of the post-larval Ammodytidae in Scottish waters is also being studied. This has been made possible by the courtesy of Dr C. E. Lucas, Director of the Marine Laboratory of the Scottish Home Department at Aberdeen, where extensive collections were made available to Mr Corbin for examination.

Mr M. D. Menon, Indian State Scholar, has studied the biology of *Gadus minutus*. In its post larval stages *G. minutus* feed entirely on copepods, mainly *Pseudocalanus elongatus*. The O-group feeds on small decapods, amphipods, copepods, isopods and polychaetes. The adolescent and adult groups feed on larger decapods like *Processa canaliculata*, *Galathea* sp. and *Portunus* sp., fish, polychaetes and amphipods. The feeding of the fish shows a seasonal fluctuation depending on spawning and growth.

The age and growth rate of the fish have been computed from the supra-occipital crests, which show alternating opaque and transparent zones. The males and females grow at the same rate in the first year; but in the succeeding years the males grow more slowly than the females. The spawning period is from February to May with the height of spawning in March and April. The majority of males reach maturity at *ca.* 11 cm. and the females at *ca.* 13 cm. Most of the fish spawn in their second spring. The results of this work are being published in Vol. XXIX, No. 1, of the *Journal*.

Mr H. W. Chang, British Council Scholar from the Academia Sinica, has been working on the biology of the dragonet, *Callionymus*. He has found that in addition to the two species *C. lyra* (L.) and *C. maculatus* (Rafin), a third species *C. fasciatus* (C. & V.), previously unrecorded off Plymouth, also occurs.

Both the otoliths and radials of the pectoral girdle can be used for age determination in these three species, but the latter are far more satisfactory than the otoliths. It has been found that the male *C. lyra* may reach 5 and the female 7 years of age, while no *C. maculatus* nor *C. fasciatus* has been found over 3 years old.

In the male *C. lyra* the onset of sexual maturity may take place in the third year, or it may be delayed until the fish is in its fourth or fifth years. Sexually mature fish have not been found less than about 20 cm. in total length. During the most intense period of the breeding season, April and May, nearly 80% of the males above 20 cm. are fully mature. The percentage of mature males falls abruptly in July and August, and it is less than 5 % in the winter. It is, therefore, probable that most of the male *C. lyra* die after one breeding season. Whether or not the female survives more than one spawning has not yet been determined.

Observations are also being made on the change in form and coloration in the male in relation to sexual maturity, *Callionymus* being remarkable for its sexual dimorphism.

The Library

The thanks of the Association are again due to many foreign Government Departments, to Universities and to other Institutions at home and abroad for copies of books and current numbers of periodicals either presented to the Library or received in exchange for the *Journal* of the Association. Thanks are also due to those who have sent books or reprints of their papers, which are much appreciated. To Prof. A. V. Hill, F.R.S., we are grateful for the gift of 18 volumes of *Harvey Lectures*, which cover the years 1924–47. Among other acquisitions, by purchase out of the Browne Bequest Fund, may be mentioned specially: William Scoresby, *An Account of the Arctic Regions, and the Journal of a voyage to the Northern Whale-Fishery*, 3 volumes; Sowinsky, *Amphipoden des Baikal Sees*, text and plates; Weber and Beaufort, *The Fishes of the Indo-Australian Archipelago*, 8 volumes; Lang, *Monographie der Harpacticiden*, 2 volumes; Harvey, *Phycologia Australica*, 5 volumes; and 3 volumes of the *Harriman Alaska Expedition Reports*.

Published Memoirs

Vol. XXVIII, No. 1, of the *Journal* was published in June 1949, No. 2 in October, and No. 3 in December.

The following papers, the outcome of work done at the laboratory, have been published elsewhere than in the *Journal* of the Association:

ALEEM, A. A., 1950. A fungus in *Ectocarpus granulosus* C. Agardh near Plymouth. *Nature*, Vol. 165, p. 119.

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AL-HUSSAINI, A. H., 1949. On the functional morphology of the alimentary tract of some fish in relation to differences in their feeding habits: Cytology and Physiology. *Quart. Journ. Micr. Sci.*, Vol. 90, pp. 323-54.

BACCI, GUIDO, 1949. Ricerche su *Asterina gibbosa* (Penn.). I. La migrazione delle gonadi. *Arch. Zool. Ital.*, Vol. XXXIV, pp. 23–9.

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BROWN, C. H., 1950. Quinone tanning in the animal kingdom. *Nature*, Vol. 165, p. 275.

GRAHAM, ALASTAIR, 1949. The molluscan stomach. *Trans. Roy. Soc. Edinb.*, Vol. LXI, pp. 737–78.

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INSTITUTION OF CIVIL ENGINEERS: Discussion on Maintenance of Maritime Works. Introductory Notes: (1) Timber Structures (by F. V. M. BELL); (2) Reinforced Concrete (by G. L. HARGREAVES); (3) Steel (by E. L. BROWNING). Maritime and Waterways Engineering Division, 1948–49, 1949.

JØRGENSEN, C. BARKER, 1949. Feeding-rates of Sponges, Lamellibranchs and Ascidians. *Nature*, Vol. 163, p. 912.

KNOWLES, FRANCIS G. W., 1950. The control of retinal pigment migration in *Leander serratus*. *Biol. Bull.*, Vol. 98, pp. 66–80.

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NICOL, J. A. C., 1948. The giant axons of Annelids. *Quart. Rev. Biol.*, Vol. 23, pp. 291–323.

NICOL, J. A. C., 1948. The function of the giant axon of *Myxicola infundibulum* Montagu. *Canad. Journ. Res.*, Vol. 26, D, pp. 212–22.

NICOL, J. A. C., SMYTH, C. N. & WHITTERIDGE, D., 1947. Conduction velocity in relation to axon diameter in *Myxicola infundibulum*. *XVII Int. Physiol. Congr.*, Oxford, 1947, pp. 243–4 (Abstract).

REES, W. J., 1950. On a giant Squid, *Ommastrephes caroli* Furtado, stranded at Looe, Cornwall. *Bull. Brit. Mus.* (*Nat. Hist*), *Zool.*, Vol. 1, pp. 31–41.

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RUSSELL, F. S., 1939. Hydromedusae. Family: Tubulariidae. Fiches d'identification du Zooplancton. No. 2, *Int. Cons. Explor. Mer*, Copenhague, 1949.

SEXTON, E. W., 1949. The multiform species *Jassa falcata* (Montagu 1808) Crustacea, Amphipoda. *Proc. Linn. Soc.*, Vol. 161, 1948–49, pp. 144–5. (Abstract of Exhibit by Dr Isabella Gordon, Linn. Soc., General Meeting, April 1949.)

THÉODORIDÈS, JEAN, 1949. Quelques publications récentes (1939–48) sur la biologie des Coléoptères des Iles Britanniques. *L'Entomologiste*, Vol. V, pp. 68–72.

THOMAS, P. KYNASTON & YOUNG, J. Z., 1949. Internode lengths in the nerves of fishes. *Journ. Anat.*, Vol. 83, pp. 336–50.

TRIPATHI, YOGENDRA R., 1949. Some new Myxosporidia from Plymouth with a proposed new classification of the order. *Parasitology*, Vol. 39, pp. 110–18.

WILSON, D. P., 1949. Animals of the sea. *Photogr. Journ.* A, pp. 195–9.

Membership of the Association

The total number of members on 31 March 1950 was 543, being 38 more than on 31 March 1949; of these the number of life members was 75 and of annual members 468. The number of Associate members is now five, Mr R. A. Todd having died during the year.

During the year Prof. H. U. Sverdrup and Prof. Hans Pettersson were elected Honorary Members.

Finance

General Fund. The thanks of the Council are again due to the Development Commissioners for their continued support of the general work of the laboratory.

Private Income. The Council gratefully acknowledge the following generous grants for the year:

From the Fishmongers' Company (£500), the Royal Society (£50), British Association (£50), Physiological Society (£30), the Cornwall Sea Fisheries Committee (£10), the Universities of London (£210), Cambridge (£125), Oxford (£100), Bristol (£50), Birmingham (£31. 10*s*.), Leeds (£20), Durham (£10. 10*s*.), Manchester (£10. 10*s*.), Nottingham (£10. 10*s*.), Exeter (£10. 10*s*.), Leicester (£10. 10*s*.), Hull (£10. 10*s*.), Southampton (£10. 10*s*.), Sheffield (£5), and the Imperial College of Science and Technology (£10).

President, Vice-Presidents, Officers and Council

The following is the list of those proposed by the Council for election for the year 1950–51:

President

Prof. JAMES GRAY, C.B.E., M.C., Sc.D., LL.D., F.R.S.

Vice-Presidents

The Earl of IVEAGH, C.B., C.M.G.
Viscount ASTOR
Sir NICHOLAS E. WATERHOUSE, K.B.E.
Sir SIDNEY F. HARMER, K.B.E., Sc.D., F.R.S.
Col. Sir EDWARD T. PEEL, K.B.E., D.S.O., M.C.
The Rt. Hon. TOM WILLIAMS, M.P.
G. P. BIDDER, Sc.D.
W. T. CALMAN, C.B., D.Sc., F.R.S.
Vice-Admiral Sir JOHN A. EDGELL, K.B.E., C.B., F.R.S.
Prof. A. V. HILL, C.H., O.B.E., Sc.D., F.R.S.
H. G. MAURICE, C.B.
E. S. RUSSELL, O.B.E., D.Sc.
Sir EDWARD J. SALISBURY, Kt., C.B.E., D.Sc., Sec. R.S.
Admiral Sir AUBREY C. H. SMITH, K.B.E., C.B., M.V.O.
A. T. A. DOBSON, C.B., C.V.O., C.B.E.

COUNCIL

To retire in 1951

Miss ANNA M. BIDDER, Ph.D.
Prof. F. W. ROGERS BRAMBELL, D.Sc., F.R.S.
J. N. CARRUTHERS, D.Sc.
O. D. HUNT
Prof. J. E. HARRIS, Ph.D.

To retire in 1952

MICHAEL GRAHAM, O.B.E.
C. E. LUCAS, D.Sc.
L. HARRISON MATTHEWS, Sc.D.
J. D. H. WISEMAN, Ph.D.
Prof. V. C. WYNNE-EDWARDS

To retire in 1953

G. E. R. DEACON, D.Sc., F.R.S.
E. FORD
F. C. FRASER, D.Sc.
F. GROSS, D.Sc.
Prof. C. M. YONGE, D.Sc., F.R.S.

Hon. Treasurer

Major E. G. CHRISTIE-MILLER, 38 Hyde Park Street, London, W. 2

Secretary

F. S. RUSSELL, D.S.C., D.F.C., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

G. P. BIDDER, Sc.D.
P. D. H. DUNN, C.M.G., O.B.E. (Ministry of Agriculture and Fisheries)
The Worshipful Company of Fishmongers:
The Prime Warden
Major E. G. CHRISTIE-MILLER
HARRISON S. EDWARDS
Prof. A. C. HARDY, D.Sc., F.R.S. (Oxford University)
J. E. SMITH, Ph.D. (Cambridge University)
Prof. H. GORDON JACKSON, D.Sc.(British Association)
H. G. MAURICE, C.B. (Zoological Society)
Prof. A. V. HILL, C.H., O.B.E., Sc.D., F.R.S. (Royal Society)

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET 31ST MARCH 1950

	£ s. d.	£ s. d.
CAPITAL RESERVE ACCOUNT:		
As at 31st March 1949		32688 8 2
SURPLUS ACCOUNT:		
As at 31st March 1949	2122 15 11	
Add: Excess of Income over Expenditure for the year ...	2217 9 9	
Transfer from Bequest Funds for purchase of Assets	308 2 10	
Donation for purchase of special apparatus	31 4 0	
	4679 12 6	
	37368 0 8	
AQUARIUM SINKING FUND:		
As at 31st March 1949	169 17 1	
Add: Donations for rebuilding Aquarium Tanks	26 17 5	
	196 14 6	
	£ s. d.	
E. T. BROWNE BEQUEST FUNDS:		
Building Fund, as at 31st March 1949 ...	50 7 1	
Less: Expenditure on Extension of Workshops transferred	25 0 0	
	25 7 1	
Library Fund, as at 31st March 1949 ...	1204 11 6	
Add: Interest on Investment	36 2 11	
	1240 14 5	
Less: Transfer to Surplus Account	87 0 0	
	1153 14 5	
Special Apparatus Fund, as at 31st March 1949	2650 18 8	
Add: Interest on Investment	79 11 7	
	2730 10 3	
Less: Transfer to Surplus Account	221 2 10	
	2509 7 5	
Scientific Publications Fund, as at 31st March 1949	2043 7 2	
Add: Interest on Investment	61 6 4	
	2104 13 6	
	5793 2 5	

	£ s. d.	£ s. d.
FIXED ASSETS, at valuations as estimated by the Director at 31st March 1950:		
Boats and Equipment:		
F.V. 'Sula'	11000 0 0	
Motor Boat 'Gammarus'	200 0 0	
Nets, Gear and General Equipment	100 0 0	
	11300 0 0	
Laboratory Apparatus, Equipment and Machinery ...	7090 0 0	
		18390 0 0
Library at valuation of Mr Ridgill Trout in January 1941, plus additions at cost		17100 0 0
Additions during year from Bequest Funds and Donations, at cost:		
Library	87 0 0	
Special Apparatus	252 6 10	
		339 6 10
		35829 6 10
STOCKS ON HAND as valued by the Director:		
Specimens	600 0 0	
Chemicals	250 0 0	
Journals	400 0 0	
		1250 0 0
GENERAL FUND INVESTMENT at Book Value £352. 2s. 3d. 2½% Treasury Stock ... ... (Market value £239. 8s. 9d.) (Last year £281. 13s. 10d.)		232 7 10
E. T. BROWNE BEQUEST FUND INVESTMENTS, at cost: £5901. 8s. 7d. 3% British Transport Stock ... ... (Market value £5252. 5s. 3d.) (Last year £5989. 19s. 0d.)		5795 3 6
COMPOSITION FEES FUND INVESTMENTS, at cost:		
£18. 8s. 6d. 2½% Treasury Stock	15 15 0	
£730. 12s. 2d. 3% British Transport Stock ... ... (Market value £662. 15s. 2d.) (Last year £685. 7s. 8d.)	715 3 2	
		730 18 2
VESSELS HIRE AND CAPITAL EXPENDITURE FUND INVESTMENT:		— —

COMPOSITION FEES FUND:					
As at 31st March 1949			667 18 2		
Add: Fees received			94 10 0		
				762 8 2	
BUILDINGS RECONSTRUCTION FUND:					
As at 31st March 1949			763 1 4		
Add: Grants received			2333 14 6		
Compensation received during year from War Damage Commission			917 6 9		
Transfer from E. T. Browne Bequest Building Fund			25 0 0		
			4039 2 7		
	£	s. d.			
Less: Expenditure during year					
Rebuilding East Wing	3333	14 6			
Equipment for East Wing	278	17 6			
			3612 12 0		
				426 10 7	
SUNDRY CREDITORS:					
Accrued Expenses			1050 4 3		
Subscriptions and Grant received in advance			183 5 0		
				1233 9 3	
				£45780 5 7	

SUNDRY DEBTORS:					
Sales of Specimens, etc.					738 10 9
PREPAYMENTS					103 18 4
VESSELS HIRE AND CAPITAL EXPENDITURE FUND:					
As at 31st March 1949			4532 16 10		
Less: Recovered during year:					
	£	s. d.			
Grant	4517	4 10			
Profit on sale of Investment	15	6 7			
Transfer from General Fund		5 5			
			4532 16 10		— —
BALANCES AT BANKS AND CASH IN HAND:					
Coutts & Co.			555 11 10		
Lloyds Bank Ltd. Plymouth...			480 3 9		
Cash in Hand...			64 4 7		
(Cr.)			—		1100 0 2
					£45780 5 7

O. D. HUNT
L. HARRISON MATTHEWS } *Members of the Council.*

REPORT OF THE AUDITORS TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

Capital expenditure on the erection of buildings on land held on lease from the War Department is excluded. Subject to the foregoing, in our opinion and to the best of our information and according to the explanations given to us, the above balance sheet and annexed income and expenditure account give a true and fair view of the state of the Association's affairs as at 31st March 1950, and of the excess of income over expenditure for the year ended on that date.

We have obtained all the information and explanations which to the best of our knowledge and belief were necessary for our audit. In our opinion the Association has kept proper books of account and the above mentioned accounts, which are in agreement therewith, give in the prescribed manner the information required by the Companies Act, 1948.

Prudential Buildings, George Street, Plymouth.
18th May 1950.

PRICE, WATERHOUSE & CO.
Chartered Accountants

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31ST MARCH 1950

	£ s. d.	£ s. d.
To SALARIES, including Association's contributions to Superannuation Scheme and National Insurance		15558 1 9
,, LABORATORY AND BOATS' CREWS' WAGES, including National Insurance, contributions to Superannuation Scheme, War Bonus and Employer's Liability Insurance		12786 6 9
,, UPKEEP OF LIBRARY		584 8 6
,, SCIENTIFIC PUBLICATIONS, *less* Sales		1202 5 3
,, UPKEEP OF LABORATORIES AND AQUARIUM:		
Buildings and Machinery	785 11 8	
Electricity, Oil, Gas, Coal and Water	556 5 4	
Chemicals and Apparatus	917 13 1	
Insurances, Tithe, Ground Rent and Rent of Store ...	134 13 5	
Travelling Expenses	588 19 3	
Audit Fee	10 10 0	
Stationery, Postages, Telephone, Carriage and Sundries	576 14 9	
Specimens	180 6 2	
		3750 13 8
,, MAINTENANCE AND HIRE OF BOATS:		
Petrol, Oil, Paraffin, etc	604 17 6	
Maintenance and Repairs to Nets, Gear and Apparatus	1884 0 2	
Boat Hire, Collecting Expenses and Upkeep of Truck	143 0 6	
Insurances	668 6 0	
Hire of R.V. 'Sabella'	1380 0 0	
		4680 4 2
,, ENTERTAINMENT EXPENSES		32 17 3
,, BANK CHARGES		26 9 3
,, BALANCE, being Excess of Income over Expenditure for the year		2217 9 9
		£40838 16 4

Note: No provision is made for replacement of Fixed Assets.

	£ s. d.	£ s. d.
By GRANTS AND TABLE RENTS:		
Ministry of Agriculture and Fisheries grant from Development Fund	34000 0 0	
Fishmongers' Company	500 0 0	
Miscellaneous (including British Association £50, Royal Society £50, Physiological Society £30, Cornwall Sea Fisheries Committee £10, Universities of London £210, Cambridge £125, Oxford £100, Bristol £50, Birmingham £31. 10*s.* 0*d.*, Leeds £20, Durham £10. 10*s.*0*d.*, Exeter £10. 10*s.*0*d.*, Leicester £10. 10*s.*0*d.* Manchester £10. 10*s.* 0*d.*, Nottingham £10. 10*s.* 0*d.*, Southampton £10. 10*s.* 0*d.*, Hull £10. 10*s.* 0*d.*, Sheffield £5, Imperial College £10, Ministry of Works £104.)	1276 0 3	
		35776 0 3
,, SUBSCRIPTIONS (excluding subscriptions received in advance)		472 11 10
,, FEES FOR TESTS OF MATERIALS		12 12 0
,, SALES:		
Specimens	2520 8 7	
Fish	361 6 8	
	£ s. d.	
Nets, Gear and Hydrographical Apparatus	1389 14 2	
Less: Cost of Materials	1164 14 3	
	224 19 11	
		3106 15 2
,, INTEREST ON INVESTMENTS		29 1 6
,, SALE OF DR M. V. LEBOUR'S BOOK		7 17 3
,, SALE OF 'PLYMOUTH MARINE FAUNA'		9 10 0
,, AQUARIUM:		
Admission Fees	1565 0 7	
Sale of Guides and Postcards	96 4 0	
	1661 4 7	
	£ s. d.	
Less: Maintenance of Buildings	37 12 4	
Printing Tickets	4 9 5	
Food	101 0 6	
Wages	93 14 0	
	236 16 3	
		1424 8 4
, TRANSFER FROM BIOLOGICAL INVESTIGATIONS ON ALGAE FUND		— — —
		£40838 16 4

LIST OF GOVERNORS, FOUNDERS, MEMBERS, HONORARY AND ASSOCIATE MEMBERS

1950

GOVERNORS

The British Association for the Advancement of Science, *Burlington House, W.* 1
The University of Oxford
The University of Cambridge
The Worshipful Company of Clothworkers, 48 *Fenchurch Street, E.C.* 3
The Worshipful Company of Fishmongers, *London Bridge, E.C.* 4
The Prime Warden. (**Council,** 1886–)
Edwards, Harrison S., *Westhumble Lacey, nr Dorking, Surrey.* (**Council,** 1950–)
Christie-Miller, Major E. G., 38 *Hyde Park Street, W.* 2. (**Council,** 1941–; **Hon. Treasurer,**1941–)
The Zoological Society of London, *Regent's Park, N.W.* 8
The Royal Society, *Burlington House, Piccadilly, W.* 1
Ministry of Agriculture and Fisheries, *St Stephen's House, Victoria Embankment, S.W.* 1
Bayly, Robert (the late). (**Council,** 1896–1901)
Bayly, John (the late)
Browne, E. T. (the late). (**Council,** 1913–19; 1920–37)
Thomasson, J. P. (the late). (**Council,** 1896–1903)
Bidder, G. P., Sc.D., *Cavendish Corner, Hills Road, Cambridge.* (**Council,** 1899–; **President,** 1939–45; **Vice-President,** 1948–)
The Lord Moyne, P.C., D.S.O. (the late). (**Vice-President,** 1929; 1939–45; **President,** 1930–39)
Allen, E. J., C.B.E., D.Sc., LL.D., F.R.S. (the late) (Honorary.) (**Council,** 1895–1942; **Secretary,** 1895–1936; **Hon. Governor,** 1937–42)

FOUNDERS

1884 The Corporation of the City of London, *The Guildhall, E.C.* 3
1884 The Worshipful Company of Mercers, *Mercers' Hall,* 4 *Ironmonger Lane, E.C.* 2
1884 The Worshipful Company of Goldsmiths, *Goldsmiths' Hall, Foster Lane, E.C.* 2
1884 The Royal Microscopical Society, *B.M.A. House, Tavistock Square, W.C.* 1
1884 Bulteel, Thos. (the late)
1884 Burdett-Coutts, W. L. A. Bartlett (the late)
1884 Crisp, Sir Frank, Bart. (the late). (**Council,** 1884–92; **Hon. Treasurer,** 1884–88)
1884 Daubeny, Captain Giles A. (the late)
1884 Eddy, J. Ray (the late)
1884 Gassiott, John P. (the late)
1884 Lankester, Sir E. Ray, K.C.B., F.R.S. (the late). (**Hon. Secretary,** 1884–90; **President,** 1891–1929)
1884 Lord Masham (the late)

1884 Moseley, Prof. H. N., F.R.S. (the late). (**Chairman of Council**, 1884–88)
1884 Lord Avebury, F.R.S. (the late). (**Vice-President**, 1884–1913)
1884 Poulton, Prof. Sir Edward B., F.R.S. (the late). (**Council**, 1888–94)
1884 Romanes, Prof. G. J., LL.D., F.R.S. (the late). (**Council**, 1884–91)
1884 Worthington, James (the late)
1885 The 15th Earl of Derby (the late)
1887 Weldon, Prof. W. F. R., F.R.S. (the late). (**Council**, 1890–1901; representing British Association, 1901–5)
1888 Bury, Henry, *The Gate House*, 17 *Alumdale Road*, *Bournemouth West*
1888 The Worshipful Company of Drapers, *Drapers' Hall*, *E.C.* 2
1889 The Worshipful Company of Grocers, *Grocers' Hall*, *Princes Street*, *E.C.* 2
1889 Thompson, Sir Henry, Bart. (the late). (**Vice-President**, 1890–1903)
1889 Lord Revelstoke (the late)
1890 Riches, T. H. (the late). (**Council**, 1920–25)
1892 Browne, Mrs E. T. (the late)
1898 Worth, R. H., M.Inst.C.E., 32 *Thornhill Road*, *Plymouth*, *Devon*
1899 The Earl of Iveagh, C.B., C.M.G., 11 *St James's Square*, *S.W.* 1. (**Vice-President**, 1929→)
1902 Gurney, Robert, D.Sc., (the late). (**Council**, 1932–5)
1904 Shaw, Joseph, K.C. (the late)
1909 Harding, Colonel W. (the late)
1910 Murray, Sir John, K.C.B., F.R.S. (the late). (**Council**, 1896–99; **Vice-President**, 1900–13)
1912 Swithinbank, H. (the late)
1913 Shearer, Dr Cresswell, F.R.S. (the late)
1913 Heron-Allen, E., F.R.S. (the late)
1918 Evans, George (the late). (**Hon. Treasurer**, 1915–31; **Vice-President**, 1925–33)
1920 McClean, Capt. W. N., 39 *Phillimore Gardens*, *W.* 8
1920 Lord Buckland of Bwlch (the late)
1920 Llewellyn, Sir D. R. (the late)
1921 Harmer, F. W. (the late)
1924 The MacFisheries, Ltd., *Ocean House*, *Pudding Lane*, *E.C.* 3
1924 Lady Murray (the late)
1925 The Institution of Civil Engineers, *Great George Street*, *Westminster*, *S.W.* 1
1925 Discovery Committee
1927 Bidder, Miss Anna M., Ph.D., *Cavendish Corner*, *Hills Road*, *Cambridge*. (**Council**, 1948→)
1933 Peel, Col. Sir Edward T., K.B.E., D.S.O., M.C., *c/o Messrs Peel and Co., Ltd.*, *P.O. Box* 331, *Alexandria*, *Egypt*. (**Vice-President**, 1936→)
1938 Buchanan, Dr Florence (the late)
1945 Brown, Arthur W. W., *Sharvells*, *Milford-on-Sea*, *Hants*

Members

* Life Members

1949 Abbott, B. C., *Biophysics Research Unit*, *University College*, *Gower Street*, *London*, *W.C.* 1
1939 Abercrombie, M., *Department of Anatomy*, *University College*, *Gower Street*, *London*, *W.C.* 1
1945 Aberdeen University Library, *The University*, *Aberdeen*

1947 Achimota College, *Department of Zoology, Achimota, Gold Coast Colony*
1934 Adam, Mrs K. M. G., 84 *Lasswade Road, Edinburgh* 9
1940 Adrian, Prof. E. D., O.M., M.D., D.Sc., LL.D., F.R.S., *St Chad's*, 48 *Grange Road, Cambridge*
1947 Affleck, R. J., 45 *Sherwood Avenue, London, S.W.* 16
1949 Aleem, A. A., Ph.D., *Faculty of Science, Farouk I University, Moharram Bey, Alexandria, Egypt*
1950 Alexandrowicz, J. S., Ph.D., M.D., *The Laboratory, Citadel Hill, Plymouth, Devon*
1949 Allen, Mrs M. E., 18 *Killieser Avenue, Streatham Hill, London, S.W.* 2
*1927 Amirthalingam, C., Ph.D., 2 *Dickmans Path, Colombo, Ceylon*
1932 Aquario Vasco da Gama, *Estação de Biologia Maritima, Cais do Sodré, Lisbon, Portugal*
1944 Ashby, D. G., *P.O. Avondale, Salisbury, S. Rhodesia*
1947 Astill, D. R. D., *Newball and Mason, Ltd., Beech Avenue, Nottingham*
*1911 Viscount Astor, 3 *Elliot Terrace, Plymouth, Devon.* (**Vice-President**, 1911→)
*1929 Atkins, Miss D., D.Sc., *Oak Cottage, Chichele Road, Oxted, Surrey*
*1939 Atkins, W. R. G., O.B.E., Sc.D., F.R.I.C., F.Inst.P., F.R.S., *The Old Vicarage, Antony, Torpoint, Cornwall*
*1910 Atkinson, G. T., *Gresham House, Esplanade, Lowestoft, Suffolk*
1950 Attridge, J., 44 *Windermere Road, Muswell Hill, London, N.* 10

1948 Baal, H. J., 3 *Bel Royal Villas, Jersey, C.I.*
1950 Baerends, Prof. G. P., *Zoological Laboratory, Reitemakersrijge* 14, *Groningen, Holland*
1949 Bagenal, T., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1939 Bahl, Prof. K. N., D.Sc., *Department of Zoology, The University, Lucknow, India*
1950 Bainbridge, R., 43 *Strathmore Avenue, Hull*
*1920 Baker, J. R., D.Sc., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1936 Baldwin, Prof. E., Ph.D. *Department of Biochemistry, University College, Gower Street, London, W.C.* 1. (**Council**, 1946–48)
1949 Barnard, E. E. P., 7 *Webster Gardens, Ealing, London, W.* 5
1939 Barnes, H., Ph.D., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1930 Barrett, W. H., *Roxeth Farm, Bessborough Road, Harrow, Middlesex*
1939 Barrington, Prof. E. J. W., D.Sc., *Department of Zoology, The University, Nottingham*
1946 Barter, W. Y., 29 *Sea View Avenue, Plymouth, Devon*
1939 Bassindale, R., *University College, Achimota, Accra, Gold Coast*
1932 Bateman, J. B., Ph.D., *Physical and Chemical Division, Camp Detrick, Frederick, Ind., U.S.A.*
1946 Batham, Miss E. J., Ph.D., *Portobello Marine Biological Station, via Port Chalmers, Otago, New Zealand*
1950 Baughman, J. L., *Texas Game, Fish and Oyster Commission, Rockport, Texas, U.S.A.*
1939 Baxter, E. W., *Biology Department, Medical School, Guy's Hospital, London, S.E.* 1
*1929 Bayliss, L. E., Ph.D., *Department of Physiology, University College, Gower Street, London, W.C.* 1
1934 Beadle, L. C., *Department of Biology, College of Medicine, University of Durham, Newcastle-upon-Tyne* 1, *Northumberland*

1928 Beer, G. R. de, D.Sc., F.R.S., *British Museum (Natural History), Cromwell Road, London, S.W.* 7
1950 Bell, Mrs E. B., 121 *Park Avenue, Hull, Yorks*
1947 Berrill, Prof. N. J., *Department of Zoology, McGill University, Montreal, Canada*
1947 Best, A. C. G., 6 *Station Road, Loudwater, High Wycombe, Bucks*
1948 Betts, Slade, 100 *Avondale Road, Bromley, Kent*
1903 Bidder, Col. H. F., *The Malting House, Nettlebed, near Henley-on-Thames, Oxon*
*1945 Bingley, F. J., *Broomhill, Herringswell, near Bury St Edmunds, Suffolk*
1925 Birkbeck College, *Fetter Lane, London, E.C.* 4
1931 Birtwistle, W., 73 *North Street, Skibbereen, Co. Cork, Eire*
1947 Bishop, M. W. H., *Meadow Farm, Waterbeach, Cambs*
1945 Black, J. A., *Ash House, Caton, near Lancaster, Lancashire*
1947 Black, Miss M. K., *c/o F. Band, High Street, Benwick, March, Cambs*
1930 Blaschko, Dr H., *Department of Pharmacology, South Parks Road, Oxford*
1910 Bloomer, H. H., *Longdown, Sunnydale Road, Swanage, Dorset*
1936 Bogue, Prof. J. Yule, D.Sc., *Heyscroft, Hartley Road, Altrincham, Cheshire*
1932 Bolitho, Capt. R. J. B., *Gorey, Jersey, C.I.*
1945 Boney, A. D., *Ivydene, Grosvenor Road, Crownhill, Plymouth, Devon*
*1933 Boschma, Prof. Dr H., *Rijksmuseum van Natuurlijke Historie, Leiden, Holland*
1947 Bossanyi, J., *Dove Marine Laboratory, Cullercoats, Northumberland*
1944 Boyd, Lt. David, R.N.V.R., 261 *Woodstock Road, Oxford*
1949 Braithwaite, E. R., *Research Department, Acheson Colloids Ltd., Prince Rock, Plymouth, Devon*
1940 Brambell, Prof. F. W. Rogers, D.Sc., F.R.S., *Department of Zoology, University College of North Wales, Bangor, Caernarvonshire.* (**Council**, 1944–47, 1948→)
1924 Brightwell, L. R., *White Cottage, Chalk Lane, East Horsley, Surrey*
1933 Bristol University, *Department of Zoology, Bristol*
1941 British Celanese Ltd., *Celanese House, Hanover Square, London, W.* 1
1948 British Cod Liver Oils (Hull and Grimsby) Ltd., *P.O. Box No.* 18, *Hull*
1939 British Ropes Ltd., *Western Avenue, Cardiff*
*1946 Brock, Mrs C. H., Ph.D., *Dept. of Agriculture, Downing St., Cambridge*
1946 Brough, Prof. James, D.Sc., *Department of Zoology and Comparative Anatomy, University College, Newport Road, Cardiff*
1928 Brown, Miss E. M., 6 *Effingham Lodge, Surbiton Crescent, Kingston-on-Thames, Surrey*
1936 Brown, Herbert H., O.B.E., Ph.D., *Manager, Fisheries Division, Colonial Development Corporation,* 33 *Dover Street, London, W.* 1
*1925 Bull, Herbert O., D.Sc., *Dove Marine Laboratory, Cullercoats, Northumberland*
1920 Burne, R. H., F.R.S., *Monkschester, Blue House Lane, Limpsfield, Surrey*
1948 Burrows, Mrs E. M., *Hartley Botanical Laboratories, The University, Liverpool* 3
1947 Burton, Miss J. M., 55 *Popes Grove, Twickenham, Middlesex*
1930 Burton, M., D.Sc., *British Museum (Natural History), Cromwell Road, London, S.W.* 7. (**Council**, 1936–39)
1947 Burton, R. F., 55 *Popes Grove, Twickenham, Middlesex*
*1949 Bush, Prof. S. F., D.Phil., *Department of Zoology, University of Natal, Pietermaritzburg, S. Africa*
1949 Butcher, A. W., *Three Salmons Hotel, Usk, Monmouthshire*

1949 Cameron, H. D., 5 *Compton Park Road, Mannamead, Plymouth, Devon*
*1950 Cameron, Prof. W. M., *Institute of Oceanography, University of British Columbia, Vancouver, Canada*
1949 Campbell, L. E., Ph.D., F.R.I.C., *British Food Manufacturing Industries Research Association, 2 Dalmeny Avenue, London, N. 7*
1920 Cannon, Prof. H. Graham, Sc.D., F.R.S., *Department of Zoology, Victoria University, Manchester.* (**Council**, 1927–30, 1932–34, 1937–41, 1942–45)
1950 Cant, Miss M. A., 8 *Clyde Road, Sutton, Surrey*
1950 Capstick, C. K., 24 *Kennersdene, Tynemouth, Northumberland*
1927 Carruthers, J. N., D.Sc., *Hydrographic Department, Admiralty, Cricklewood, London, N.W. 2.* (**Council**, 1948→)
1923 Carter, G. S., Ph.D., *Department of Zoology, Downing Street, Cambridge*
1948 Carthy, J. D., *Department of Zoology, Downing Street, Cambridge*
*1931 Cattell, Dr McKeen, *Cornell University Medical College, 477 First Avenue, New York City, U.S.A.*
*1948 Cattley, J. G., *Fisheries Laboratory, Lowestoft, Suffolk*
1949 Centre de Recherches et d'Etudes Océanographiques, 1 *rue Victor Cousin, Paris (Ve), France*
*1949 Chang, H. W., *c/o The Laboratory, Citadel Hill, Plymouth, Devon*
*1949 Chapman, Garth, Ph.D., 12 *Wave Crest, Whitstable, Kent*
1936 Charterhouse School, *Biological Department, Godalming, Surrey*
1947 Cheng, Prof. Chung, Ph.D., *Department of Oceanography, National Amoy University, Amoy, China*
*1947 Chidambaram, K., *Fisheries Biological Station, West Hill Post, South Malabar, India*
1946 Chipperfield, Philip N. J., Ph.D., *Hillside, Manor Road, Brixham, Devon*
1942 Christie-Miller, Major E. G., 38 *Hyde Park Street, London, W. 2.* (**Council** 1941→; **Hon. Treasurer**, 1941→)
1950 Clair, C. le, *Glebe Cottage, Cornwood, Ivybridge, S. Devon*
1947 Clarke, Miss D. H., *Gowdhurst, Chart Lane, Dorking, Surrey*
1949 Clarke, K. U., 7 *Stanley Avenue, Wembley, Middlesex*
1944 Clarke, Robert H., *'Discovery' Investigations, Queen Anne's Chambers, 41 Tothill Street, London, S.W. 1*
1936 Clothier, Peter, *Hill Close, Street, Somerset*
1939 Clowes, A. J., *Division of Fisheries, Beach Road, Sea Point, Cape Town, S. Africa*
*1886 Coates and Co. (Plymouth), Ltd., *Black Friars Distillery, Southside Street, Plymouth, Devon*
*1945 Cobham, Lt.-Cdr. A. J., R.N., *Noel Cottage, Castle Street, Portchester, Hants*
*1925 Cockshott, Lt.-Col. A. M., R.A.S.C., *Cotteswold Naturalists' Field Club, City Library, Gloucester*
1933 Cole, H. A., D.Sc., *Fisheries Experiment Station, Castle Bank, Conway, Caernarvonshire*
1948 Collier, Albert, *c/o Fish and Wildlife Service, Ft Crockett, Galveston, Texas, U.S.A.*
*1885 Collier and Co., 53 *Southside Street, Plymouth, Devon*
1950 Collins, William N., 603 *Thatcher Avenue, River Forest, Illinois, U.S.A.*
1947 Collis, Miss M. M., 27 *Mowbray Road, Cambridge*
1930 Colman, J. S., *Marine Biological Station, Port Erin, Isle of Man*
1947 Cook, Miss P. M., 51 *Runnymede Crescent, Streatham, London, S.W. 16*
1940 Cook, R. H., 24 *Luard Road, Cambridge*
1939 Cooper, Major Brian, *Countess Weir House, Countess Weir, Exeter, Devon*

*1933 Cooper, L. H. N., D.Sc., F.R.I.C., *The Laboratory, Citadel Hill, Plymouth, Devon*
1937 Corbin, P. G., *The Laboratory, Citadel Hill, Plymouth, Devon*
1937 Corbin, Mrs P. G., Ph.D., *Dostabrook, Horrabridge, S. Devon*
1946 Corlett, John, M.Sc., *Fisheries Laboratory, Lowestoft, Suffolk*
1937 Cosway, C. A., *South Devon Technical College, Teignmouth Road, Torquay, S. Devon*
1941 Cott, H. B., D.Sc., *University Museum of Zoology, Cambridge*
1948 Council for Promotion of Field Studies, *Dale Fort Field Centre, Haverfordwest, Pembs*
1936 Crawford, G. I., 18 *East Drive, Carshalton Beeches, Surrey*
*1928 Crew, Prof. F. A. E., M.D., D.Sc., F.R.S., *Usher Institute, Warrenden Park Road, Edinburgh* 9
1929 Crofts, Miss D. R., D.Sc., *Deerbank, Noisey Wood, Billericay, Essex*
*1930 Cuthbertson, Norman, 101 *Johnstone Avenue, Dartmouth, Nova Scotia, Canada*

1922 Dale, Sir Henry H., O.M., G.B.E., F.R.C.P., LL.D., F.R.S., *The Wellcome Trust, 28 Portman Square, London, W. 1.* (**Council**, 1922–28)
1948 Dales, R. Phillips, 67 *Westmoreland Avenue, Squirrels Heath, Essex*
1947 Dall, William, *Grace Street, Corinda, S.W. 4, Brisbane, Queensland, Australia*
*1919 Damant, Capt. G. C. C., C.B.E., R.N., *Thursford, Cambridge Road, East Cowes, I. of W.* (**Council**, 1928–31, 1937–40)
1939 Danielli, Prof. J. F., D.Sc., *Department of Zoology, King's College, Strand, London, W.C. 2.* (**Council**, 1944–45)
1947 Danmarks Akvarium, *Charlottenlund, Denmark*
1929 Darby, Dr H. H., *Carnegie Institution of Washington, 5241 Broad Branch Road, N.W., Washington 15, D.C., U.S.A.*
1948 Dartmouth, The Royal Naval College
1946 Das, S. M., D.Sc., *Central Marine Fisheries Research Station, West Hill P.O., Calicut, S. India*
1920 Davidson, Dr W. Cameron, *Avonleigh, Acadia Road, Torquay, S. Devon*
1931 Dawes, B., D.Sc., *Department of Zoology, University of London, King's College, Strand, London, W.C. 2*
1944 Day, Prof. J. H., D.F.C., *Department of Zoology, University, Rondebosch, Cape Town, S. Africa*
1948 Day, Lionel E., 24 *Inverness Avenue, Westcliff-on-Sea, Essex*
1948 Day, Peter R., 36 *Templeton Avenue, Chingford, London, E. 4*
1938 Deacon, G. E. R., D.Sc., F.R.S., 55 *Broadhurst, Ashtead, Surrey.* (**Council**, 1946–49, 1950→)
1939 Dennell, Ralph, *Department of Zoology, The University, Manchester* 13
*1915 Dick, G. W., J.P., 500 *Manning Road, Durban, Natal, S. Africa*
1944 Digby, P. S. B., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1948 Dodd, J. M., *Gatty Marine Laboratory, The University, St Andrews, Fife*
1942 Dollner, H., 3516 *Northcliffe, Montreal, N.D.G., Canada*
1949 Doochin, Herman D., *School of Biological Science, Stanford University, Stanford, California, U.S.A.*
1946 Douglas, Leslie, 11 *Harbour View, Seahouses, Northumberland*
1940 Dowson, Capt. W. B., *c/o Department Commerce and Industry, Freetown, Sierra Leone*
1946 Duly, S. J., 68 *Richmond Hill Court, Richmond, Surrey*
1939 Dundee University College Library, *Dundee, Forfar*

1947 Dunne, B., 53 *Headland Park, Plymouth, Devon*
1949 Dussart, B. H., *Le Paraclet par Boves (Somme), France*
1937 Dyke, Frederick Montague, *Branksome, Boreham Wood, Elstree, Herts*

*1934 Eales, Miss N. B., D.Sc., *Zoology Department, The University, Reading*
1933 Eastham, Prof. L. E. S., *Department of Zoology, The University, Sheffield* 10
1945 Edgell, Vice-Admiral Sir John A., K.B.E., C.B., F.R.S., 1 *Glenalmond House, Manor Fields, Putney, London, S.W.* 15. (**Council**, 1945–48, **Vice-President**, 1948–)
1927 Eggleton, P., D.Sc., *Department of Physiology, The University, Edinburgh*
1928 Egypt: Coastguard and Fisheries Service, *Alexandria, Egypt*
1948 Elgood, J. H., 159 *Purley Oaks Road, Sanderstead, Surrey*
1950 Elliott, Mrs J. H., 39 *Woodhaw, Egham, Surrey*
*1929 Elmhirst, L. K., *Dartington Hall, Dartington, near Totnes, S. Devon*
1931 Enoch, C. E. D., *Rayman Lodge, Sherborne Road, Parktown, Johannesburg, S. Africa*
*1947 Evans, Miss G. C., *Gerrans, Portscatho, near Truro, Cornwall*
*1923 Evans, W. Edgar, 38 *Morningside Park, Edinburgh*
1942 Ewer, D. W., *Department of Zoology, Natal University College, P.O. Box* 375, *Pietermaritzburg, Natal, S. Africa*

*1929 Faouzi, Dr Hussein, *Faculty of Science (Department of Zoology), Farouk I University, Moharram Bey, Alexandria, Egypt*
1948 Faulkner, I. J., Ph.D., *I.C.I. Billingham Division, Billingham, E. Durham*
1950 Featherstone, Miss M. J., 3 *Clarence Road, Bickley, Kent*
*1933 Fellowes, Miss Rosalind, 23 *The Cloisters, Windsor Castle, Berks*
1950 Fisher, L. R., 23 *Langton Avenue, Chelmsford, Essex*
1940 Foote, Miss V. V. J., *Achimota College, Achimota, Gold Coast Colony*
1928 Ford, E., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*. (**Council**, 1950–)
1935 Ford, E. B., D.Sc., F.R.S., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1939 Forrest, J. E., *Department of Zoology, Queen Mary College, Mile End Road, London, E.* 1
1950 Forster, G. R., *The Laboratory, Citadel Hill, Plymouth, Devon*
1949 Fountain, H. C., *The Store Cottage, Polbathic, Torpoint, Cornwall*
1912 Fox, Prof. H. M., F.R.S., *Bedford College for Women, Sussex Lodge, Regent's Park, London, N.W.* 1. (**Council**, 1928–30, 1931–34, 1944–47)
1942 Foxon, G. E. H., *Department of Biology, Guy's Hospital Medical School, London Bridge, London, S.E.* 1
1950 Frampton, Cdr. R. H. C. F., R.N. (Rtd), *Ministry of Agriculture and Fisheries, Citadel Hill, Plymouth, Devon*
1924 Fraser, Miss E. A., D.Sc., *Department of Zoology, University College, Gower Street, London, W.C.* 1
1935 Fraser, F. C., D.Sc., *British Museum (Natural History), Cromwell Road, London, S.W.* 7. (**Council**, 1950–)
*1935 Fraser, James H., Ph.D., *Marine Laboratory, Wood Street, Torry, Aberdeen*
*1939 Fretter, Miss Vera, Ph.D., *Department of Zoology, Birkbeck College, Fetter Lane, London, E.C.* 4
*1930 Fritsch, Prof. F. E., D.Sc., F.R.S., 34 *Causewayside, Cambridge*. (**Council**, 1931–34, 1937–40, 1943–46)

1949 Fuller, A. S., 114 *Vale Road, Worcester Park, Surrey*
1948 Furness, W. J., *Inglewood, Abbey Park Road, Grimsby, Lincs.*

1941 Gardiner, Mrs A. C., *c/o Mrs Walter Gardiner*, 4 *Grange Road, Cambridge*
1949 Gates, J. T., 19 *Fircroft Road, Hook Rise, Surbiton, Surrey*
*1928 Gates, Prof. R. R., D.Sc., LL.D., F.R.S., *Biological Laboratories, Harvard University, Cambridge* 38, *Mass., U.S.A.*
1948 Gatty Marine Laboratory, (The Principal), *The University, St Andrews, Fife*
1947 Gay, Miss M. V., *Lowerfield, Lapford, N. Devon*
1935 Gilson, H. Cary, *Freshwater Biological Association, The Ferry House, Far Sawrey, Ambleside, Westmorland.* (**Council**, 1940–43, 1947–50)
1945 Glasgow University, Zoology Department, *Glasgow, W.* 2
1946 Glover, R. S., *Department of Oceanography, University College, Hull*
1950 Goodley, E. F. W., 2 *Thickthorn Lane, Laleham, Staines, Middlesex*
1939 Goodrich, Dr Helen Pixell, 12 *Park Town, Oxford*
1939 Gordon, Miss Isabella, D.Sc., *British Museum (Natural History), Cromwell Road, London, S.W.* 7
1943 Gourock Ropework Co., Ltd., 92 *Bay Street, Port Glasgow, Renfrew*
1931 Graham, Prof. Alastair, D.Sc., *Department of Zoology, Birkbeck College, Fetter Lane, London, E.C.* 4
1949 Graham, F. G., *Trethake, Plymstock Road, Oreston, near Plymouth, Devon*
1931 Graham, Michael, O.B.E., *Fisheries Laboratory, Lowestoft, Suffolk.* (**Council**, 1931–32, 1933–36, 1943–46, 1949→)
1930 Gray, Sir Archibald M. H., C.B.E., M.D., F.R.C.P., F.R.C.S., 39 *Devonshire Place, London, W.* 1
1912 Gray, Prof. J., C.B.E., M.C., Sc.D., LL.D., F.R.S., *Department of Zoology, Downing Street, Cambridge.* (**Council**, 1920–24, 1928→; representing Cambridge University, 1928–45; **President**, 1945→)
1943 Great Grimsby Coal, Salt and Tanning Co., *Fish Dock Road, Grimsby, Lincs*
1949 Green, J., 61 *Ruskin Road, Crewe, Cheshire*
1950 Greenfield, Leonard J., 1262*E Walsh Avenue, University Branch, Miami* 46, *Florida, U.S.A.*
1948 Grigg, Miss Ursula M., *Dove Marine Laboratory, Cullercoats, Northumberland*
1948 Grove, A. V., 86 *Gowar Road, Sketty, Swansea, Glam*
1947 Guiler, E. R., *Department of Zoology, University of Tasmania, Hobart, Tasmania*
1947 Gundry, Joseph, and Co., *Bridport, Dorset*

1946 Haifa: *Sea Fisheries Research Station, P.O. Box* 50, *Haifa, Palestine*
1950 Haines, Surg.-Lieut. D. O., R.N., 217 *Cliffe Road, Strood, Rochester, Kent*
1949 Hall, Miss N. F., *Tyne Brand Products Ltd., North Shields, Northumberland*
*1946 Hamond, Richard, *Morston, Holt, Norfolk*
1947 Harbott, A. J., *Wensleydale*, 7 *Manorcrofts Road, Egham, Surrey*
1923 Hardy, Prof. A. C., D.Sc., F.R.S., *Department of Zoology and Comparative Anatomy, University Museum, Oxford.* (**Council**, 1938–41, 1942→; representing Oxford University, 1946→)
1929 Harington, Sir Charles R., Ph.D., F.R.S., *National Institute of Medical Research, The Ridgeway, Mill Hill, London, N.W.* 7
1950 Harley, Miss M. B., *Department of Zoology, University Science Laboratories, South Road, Durham*
1946 Harling, Miss K. E., *The Arches, Looe, Cornwall*

*1885 Harmer, Sir Sidney F., K.B.E., Sc.D., F.R.S., 5 *Grange Road, Cambridge*. (**Council**, 1895–1912, 1918–23, 1925–44; representing Royal Society, 1925–44; **Vice-President**, 1934→)

1932 Harris, Prof. J. E., Ph.D., *Department of Zoology, The University, Bristol*. (**Council**, 1946–49, 1950→)

1946 Harris, T. R., 31 *All Saints Road, Wyke Regis, Weymouth, Dorset*

1939 Harrison, R. J., D.Sc., M.R.C.S., L.R.C.P., *Vinicombe, The Woodlands, Farnborough, Kent*

1947 Harrow Lower School Biology Department, *Lower School of John Lyon, Harrow, Middlesex*

1929 Hart, T. J., D.Sc., *c/o The Laboratory, Citadel Hill, Plymouth, Devon*

1934 Hartley, P. H. T., *Edward Gray Institute of Field Ornithology*, 91 *Banbury Road, Oxford*

1924 Harvey, H. W., Sc.D., F.R.S., *The Laboratory, Citadel Hill, Plymouth, Devon*

1933 Harvey, Prof. L. A., *Department of Zoology, University College of the South West, Exeter, Devon*. (**Council**, 1940–43)

1950 Haswell, G. A., 23 *Russell Avenue, Hartley, Plymouth, Devon*

1939 Hayes, Dr F. R., *Dalhousie University, Halifax, N.S., Canada*

1939 Hayes, Mrs F. R., *Dalhousie University, Halifax, N.S., Canada*

1950 Hazevoet, A. C., *Vogelenzangstraat* 19-*I, Amsterdam West, Holland*

1949 Heaysman, Miss J. E. M., 69 *Brook Road, Merstham, Surrey*

1948 Hedley, Ronald H., *Armstrong House, Meadowfield, Durham*

1931 Henderson, G. T. D., D.S.C., Ph.D., *Oceanographic Laboratory*, 23 *Sandport Street, Leith, Edinburgh* 6

1939 Henry, Dr Herbert G. M., *Doune Cottage, Macduff, Banffshire*

1925 Hentschel, C. C., 7 *Dudley Court, Upper Berkeley Street, London, W.* 1

1939 Herklots, G. A. C., Ph.D., *Vanners, Chobham, Surrey*

1950 Herring Industry Board, 1 *Glenfinlas Street, Edinburgh* 3

1939 Hewer, H. R., Assistant Professor, *Department of Zoology, Imperial College of Science, London, S.W.* 7

1926 Hickling, C. F., Sc.D., *Colonial Office, Sanctuary Buildings, Great Smith Street, London, S.W.* 1. (**Council**, 1947–50)

1926 Hill, Prof. A. V., C.H., O.B.E., Sc.D., F.R.S., 16 *Bishopswood Road, Highgate, London, N.* 6. (**Council**, 1925–29, 1930–33, 1934–37, 1938–41, 1942→; representing Royal Society, 1944→; **Vice-President**, 1948→)

*1949 Hill, D. K., *Postgraduate Medical School of London, Ducane Road, London, W.* 12

1939 Hill, M. D., *Uplands, near Ledbury, Herefordshire*

1947 Hill, M. N., 6 *St Eligius Street, Cambridge*

*1921 Hindle, E., Sc.D., F.R.S., *Zoological Society of London, Regent's Park, London, N.W.* 8. (**Council**, 1946–49)

1937 Hinton, M. A. C., F.R.S., 23 *Polworth Road, Streatham, London, S.W.* 16

1926 Hobson, Prof. A. D., *King's College, Newcastle-upon-Tyne* 1, *Northumberland*

1948 Hockley, A. R., *University College, Southampton*

1939 Hodgkin, A. L., F.R.S., *Trinity College, Cambridge*

1945 Hodson, W., *Rhodena, Penare Avenue, Prestatyn, Flints*

1947 Hollowday, E. D., F.R.M.S., 45 *Manor Road, Aylesbury, Bucks*

1948 Holme, N. A., *The Laboratory, Citadel Hill, Plymouth, Devon*

1939 Holmes, W., D.Phil., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*

1948 Holsgrove, H. E., 67 *Bridwell Road, Weston Mill Estate, Plymouth, Devon*

1933 Horne, F. R., *National Institute of Agricultural Botany, Huntingdon Road, Cambridge*

1950 Howard, G. H., 131 *Corporation Road, Grimsby, Lincs*
1948 Howe, Surg. Lt.-Cdr. (D) D. C., R.N., 607 *Dorchester Road, Broadway, near Weymouth, Dorset*
1950 Howells, D. V., 42 *Radstock Road, Reading, Berks*
1932 Howes, N. H., *Department of Zoology, University College, Gower Street, London, W.C.* 1
1928 Hunt, O. D., *Corrofell, Newton Ferrers, S. Devon.* (**Council**, 1944–47, 1948–)
1947 Hunter, W. Russell, *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
*1947 Hurrell, H. G., J.P., *Moorgate, Wrangaton, S. Devon*
1939 Hurst, C. P., *Landulph Rectory, Saltash, Cornwall*
*1920 Hutton, J. Arthur, *Woodlands, Alderley Edge, Manchester*
1912 Huxley, Julian S., D.Sc., F.R.S., 31 *Pond Street, London, N.W.* 3. (**Council**, 1920–25)

1946 Iceland: *Atvinnudeild Háskólans (Fiskideild), Reykjavik*
1945 Imperial Chemical Industries Ltd., *Nobel House*, 2 *Buckingham Gate, London, S.W.* 1

1945 Jefferies, H. S., 6 *Forester Road, Bath*
1949 Jellinek, P. H., *Oakdene, Christchurch Road, London, S.W.* 14
1935 Jenkin, Miss P. M., *Department of Zoology, The University, Bristol*
1934 Jepps, Miss M. W., D.Sc., *Department of Zoology, The University, Glasgow*
1949 Jeremy, W. H. R., 38 *Barnfield Road, Exeter, Devon*
1937 Jersey: Conservateur honoraire du Musée de la Société Jersiaise
*1924 Jesus College, *Oxford*
*1947 John, C. C., D.Sc., *The Aquarium, Trivandrum, S. India*
1934 John, D. Dilwyn, D.Sc., *National Museum of Wales, Cardiff*
*1947 Johnson, D. S., 10 *St John's Road, Cambridge*
1944 Johnson, Dr F. R., *Osu Fisheries Station, P.O. Box* 630, *Accra, Gold Coast Colony*
1948 Jones, C. Burdon, *Department of Zoology, University College of N. Wales, Bangor, Caern*
*1949 Jones, E. W. Knight, *Marine Biological Station, University College of N. Wales, Bangor, Caern*
1949 Jones, F. R. Harden, 9 *Clifton Crescent, Folkestone, Kent*
1948 Jones, J. D., *Nantyci, Llysonnen Road, Carmarthen, S. Wales*
1946 Jones, L. W. G., *Seymour House, Mount Wise, Plymouth, Devon*
1946 Jones, N. S., *Marine Biological Station, Port Erin, Isle of Man*
1949 Jones, R. J., 14 *Canning Road, Croydon, Surrey*
1936 Jones, Rodney R. M., *Tros-yr-Afon, Penmon, Anglesey*
1946 Jones, Prof. R. V., C.B., C.B.E., D.Phil., F.Inst.P., *Department of Natural Philosophy, Marischal College, Aberdeen*
1947 Jörgensen, C. Barker, *Slettevej* 8, *Copenhagen Söborg, Denmark*
1923 Judge, J. J., *Virginia House, Palace Street, Plymouth, Devon*
1950 Juniper, A. J., *The Polytechnic, Regent Street, London, W.* 1

1948 Katterns, L. B., 115 *Feltham Hill Road, Ashford, Middlesex*
1945 Katz, Max, 1915E, *Spruce Street, Seattle* 22, *Washington, U.S.A.*
1940 Keilin, Prof. D., Sc.D., F.R.S., *Molteno Institute, Cambridge.* (**Council**, 1940–43)
1950 Keir, Ronald S., 51 *Clincort Road, Glasgow, S.* 2

1946 Kelley, D. F., 17 *Bainbridge Avenue, Hartley, Plymouth, Devon*
1949 Kennedy, G. Y., F.R.I.C., *Department of Cancer Research, University Field Laboratory, Blackbrook Road, Sheffield* 10
1946 Kenya: The Game Warden, *Game Department, P.O. Box* 241, *Nairobi*
1950 Keynes, R. D., Ph.D., *Physiological Laboratory, Cambridge*
1949 Kimmins, B. J., 19 *Crdnleigh Gardens, Bristol* 9
1928 King, Mrs A. Redman, *Mixton House, Lerryn, Lostwithiel, Cornwall*
1947 Kingsbridge Modern Secondary School, *Kingsbridge, S. Devon*
1949 Kingston Technical College, *Kingston Hall Road, Kingston-upon-Thames, Surrey*
1927 Kirtisinghe, P., *Department of Zoology, University of Ceylon, Colombo* 3, *Ceylon*
1930 Kitching, J. A., O.B.E., Ph.D., *Department of Zoology, The University, Bristol*
1939 Knight, Miss Margery, D.Sc., *University Hall for Women Students, Holly Road, Fairfield, Liverpool.* (**Council**, 1943–46)
1945 Knowles, F. G. W., D.Phil., *Marlborough College, Marlborough, Wilts*
1948 Kow, Tham Ah, *c/o Fisheries Department, 4th Floor, Fullerton Building, Singapore*
1949 Kristensen, Dr Ingvar, *Zoölogisch Station, den Helder, Holland*

1950 La Rochelle, Station Océanographique, *Pavillon du Port-Le Gabut, La Rochelle* (*Charente-Maritime*), *France*
1950 Lasker, Reuben, *Marine Laboratory, Miami University, Coral Gables, Florida, U.S.A.*
*1925 Lebour, Miss M. V., D.Sc., *Kean Hill, Cawsand, near Plymouth, Devon*
1947 Leehane, J. D. B., 14 *Wyndham Street East, Plymouth, Devon*
1935 Le Mare, D. W., *Fisheries Department, Federation of Malaya and Singapore, Penang, Malaya*
1948 Letts, J. K., 183 *Windmill Lane, Greenford, Middlesex*
1948 Lloyd, A. T., *Wynona, Beacon Park Road, Plymouth, Devon*
1949 Lodge, Miss S. M., *Marine Biological Station, Port Erin, Isle of Man*
1948 Lovegrove, T., 2 *Athenaeum Place, The Hoe, Plymouth, Devon*
1926 Lowndes, A. G., Sc.D., F.R.I.C., *c/o The Laboratory, Citadel Hill, Plymouth, Devon*
1931 Lucas, C. E., D.Sc., *Marine Laboratory, Wood Street, Torry, Aberdeen.* (**Council**, 1949–)
1930 Lumley, Adrian, *Sunnyside, Castle Gardens, Torquay, Devon*
1938 Lysaght, Miss A. M., Ph.D., 6 *Cumberland Gardens, London, W.C.* 1

1938 MacDonald, R., 112 *Antrim Road, Belfast, N. Ireland*
1935 Mackenzie, Col. W., O.B.E., *c/o Messrs Peel and Co. Ltd., P.O. Box* 331, *Alexandria, Egypt*
1929 Mackinnon, Prof. D. L., D.Sc., 44 *St Leonard's Terrace, Chelsea, London, S.W.* 3. (**Council**, 1938–42)
1937 Mackintosh, N. A., C.B.E., D.Sc., 7 *Hinde House, Hinde Street, London, W.* 1. (**Council**, 1946–49)
1947 Macnae, William, *Department of Zoology, Rhodes University College, Grahamstown, S. Africa*
*1925 Magdalen College, *Oxford*
1945 Maitland-Adams, C. W., *The Old Rectory, Hawkwell, Hockley, Essex*
1948 Mansfield, A. W., 32 *Newton Road, Wimbledon, London, S.W.* 19

*1928 Manton, S. M., Sc.D., F.R.S. (Mrs J. P. Harding), 18 *Ennerdale Road, Richmond, Surrey*
1948 Marcotte, Alexandre, D.Sc., *Faculté des Sciences, Boulevard de l'Entente, Quebec, Canada*
1948 Mardon, Jasper, *Selwyn College, Cambridge*
1939 Marr, J. W. S., 28 *Cromwell Court, Kingston Hill, Surrey*
1949 Marshall, Douglas, M. P., *Lanwithan House, Lostwithiel, Cornwall*
*1947 Marshall, Miss S. M., D.Sc., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1939 Matthews, L. Harrison, Sc.D., *Department of Zoology, The University, Bristol.* (**Council**, 1944–47, 1949→)
1937 Mayne, Dr Cyril F., O.B.E., F.R.C.S., *c/o Barclays Bank Ltd., Plymouth, Devon*
1949 McCarthy, Miss D. F., 70 *Halton Terrace, Kensington Park, Adelaide, S. Australia*
1910 McClean, Capt. W. N., 39 *Phillimore Gardens, London, W.* 8
*1929 McEwen, Mrs Lawrence, 15 *Blackett Place, Edinburgh*
1948 McIntyre, A. D., *Marine Laboratory, Wood Street, Torry, Aberdeen*
1950 McIntyre, J. M., 75 *Harcourt Terrace, Kensington, London, S.W.* 10
*1948 Menon, M. Devidas, *Parvathi Nivas, Diwans Road, Ernakulam, United States of Cochin and Travancore, S. India*
1950 Messenger, K. G., *Uppingham School, Rutland*
1939 Metropolitan Water Board, 177 *Rosebery Avenue, London, E.C.* 1
1947 Miami University Marine Laboratory, *Coral Gables, Florida, U.S.A.*
1923 Milford Haven Trawler Owners Association, Ltd., *Milford Haven, Pembs*
1949 Millar, R. H., Ph.D., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1946 Miller, Cyril J., 42 *Westbourne Road, Peverell, Plymouth, Devon*
1949 Millott, Prof. N., Ph.D., *Department of Zoology, University College of West Indies, Mona, Liguanea, Jamaica*
1949 Mistakidis, M. N., *Oyster Research Station, Burnham-on-Crouch, Essex*
1947 Mitchell, E. S., *Hillside, Chapel Street, Camelford, Cornwall*
1947 Mitra, G. N., *Assistant Director of Fisheries, Cuttack (Orissa), India*
1940 Moore, Hilary B., Ph.D., *Marine Laboratory, Miami University, Coral Gables, Florida, U.S.A.*
1949 Morrish, Miss C. A., *Ormdale, Woodhall Avenue, Pinner, Middlesex*
1949 Morton, J. E., *Department of Zoology, Birkbeck College, Fetter Lane, London, E.C.* 4
1931 Mount Desert Island Biological Laboratory, *Salisbury Cove, Maine, U.S.A.*
1938 Mowbray, Louis L., *Curator, Bermuda Government Aquarium, Flatts, Bermuda*
1942 Moynahan, Dr E. J., *Wayside, Jordans, near Beaconsfield, Bucks*
1933 Neale, Morley H., *Chaffcombe House, Chard, Somerset.* (**Council**, 1934–36, 1939–42, 1943–46, 1947–50)
1934 Neale and West, *Trawler Owners, Wharf Street, Cardiff*
1939 Needham, Joseph, Sc.D., F.R.S., *Gonville and Caius College, Cambridge*
1947 Newell, G. E., Ph.D., 11 *Wave Crest, Whitstable, Kent*
1947 Newton, Prof. Lily, Ph.D., *Department of Botany, University College of Wales, Aberystwyth, Cardigan.* (**Council**, 1947–50)
1930 Nicholls, A. G., Ph.D., *Stowell, Hobart, Tasmania*

1950 Nicol, J. A. C., D.Phil., *Trevean, George Lane, Plympton St Maurice, S. Devon*
1947 Nisbet, R. H., 169 *Stapleton Hall Road, Finsbury Park, London, N.* 4
1948 Nobbs, Miss G. E. D., 4 *Clifton Estate, Plympton, Devon*
1949 Norris, E., *Ewdis, Priory Road, Lower Compton, Plymouth, Devon*
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Walter Garstang

WALTER GARSTANG, 1868–1949

The death of Professor Walter Garstang, at the age of 81, on 23 February 1949, broke the last living link with the foundation of our Plymouth Laboratory. It is fitting that some record of his life should be found in the pages of our *Journal*; not only because he was one of the pioneers of marine biology in this country and one of the founders of fisheries research, but particularly by reason of his having taken such a prominent part in the early history of our Association. He was on the staff of our laboratory the day it opened, and in 1895 he initiated the first of the Easter Classes which ever since have made such an important contribution to the education of British zoologists. He continued to conduct these classes until 1901 when he became director of the fishery investigations undertaken by the M.B.A. on behalf of the government, as England's share in the then new International Investigations. Apart from his marine work, Garstang made fundamental contributions to biological theory, as in his paedomorphosis conception, and for more than half a century was one of the outstanding personalities of British Zoology.

In 1938, Garstang began to write an account of his experiences in fifty years of marine biology, but with other occupations in research and the coming of the war he abandoned it. Of what he wrote, however, he left some eighty pages of typescript describing the early days at Plymouth from 1888 to 1900; these have been deposited in the library of the Plymouth Laboratory for the benefit of those interested in our early history. I feel I cannot do better than begin this brief account of his life than by quoting the opening paragraphs of this fragment of his autobiography; here we have a vivid impression of the opening not only of his career but of that of our precious laboratory. It will serve, too, as some indication of what is in store for those who delve further into this very personal account of marine zoology in the nineties.

Fifty years ago, on June 21, 1888, having taken my degree at Oxford in the morning, I journeyed to Plymouth, picking up the old broad-gauge express at Swindon, to begin duty as Secretary and Assistant to the Director of the newly founded laboratory of the Marine Biological Association. It was to be only a temporary engagement,—to me a year or so for recuperation after a serious breakdown, to the Director some biological help at the outset, which otherwise he could not expect to get at the salary of clerk-assistant sanctioned by the Council (£80). The new Director was G. C. Bourne, then and long afterwards well known as a rowing Blue and coach, eventually (1906–1921) as Linacre Professor at Oxford, who, on returning from an expedition to the coral island of Diego Garcia, had been our demonstrator in the morphological laboratory. He had suggested this arrangement upon his appointment in April, and, after consultation with my people, I had gratefully accepted it. Bourne left Oxford early in June, and I was to follow immediately after my examinations and the taking of my degree. Our joint immediate task was to get the laboratory, which was still in the hands of contractors, ready for a ceremonial opening on June 30th. We took our coats off to it. My diary

records that on the 26th both of us were in shirt sleeves cleaning a heap of dirty collecting jars,—Bourne, the great 'Beejar' of the towing path! It's a man's valet who knows him best. Next day Bourne had to break off to attend a Council meeting in London. On his return he was delighted to find the laboratory washed down, in fair order, and with a red carpet on the stairs ready for the opening.

The ceremony went off without a hitch, or, as Lankester put it in a letter to Bourne, 'Everything went off splendidly on Saturday'. The weather was superb, the speeches were cheerful, the Fishmongers' Company gave a lunch in the Grand Hotel with wine from their own cellars, the Port Admiral lent his yacht for a trip, and everyone was in high spirits. All this, however, is on permanent record in the chronicles of the Association (*Journ. Mar. Biol. Soc.*, O.S., pp. 125–141). What is not recorded is that at Bourne's request I had put out an exhibit of living things under microscopes and otherwise in the main laboratory, and that after spending some minutes in expounding the life-history of *Obelia* to a portly and insistent visitor, whom I took to be a Fishmonger, the latter interrupted me to say, 'Very interesting! I suppose you don't know who I am?' 'I'm sorry, sir, No,' I said. 'I am Professor Lankester!' Thus I met the man who was largely to rule my destinies, and those of most other young zoologists, for the next 20 years.

He was born on 9 February 1868, the eldest son of Dr Walter Garstang of Blackburn, and was educated at Blackburn Grammar School and Jesus College, Oxford. He came up to the University with a scholarship in 1884, when only $16\frac{1}{2}$, intending to read medicine. At heart he was a poet and a lover of nature. A new world opened before him as he came under the influence of that great Challenger naturalist, H. N. Moseley, who was then the Linacre Professor. He very soon decided to join the honours school of Zoology. He was only 20 when he took his degree and, as just recorded, joined Bourne at Plymouth a week before the laboratory opened in 1888. He had not then finally decided to give up a medical career, but the fascination of marine life at Plymouth was soon to cause him to do so. In 1891, he left the Plymouth staff for a year to go to Manchester as Berkley Research Fellow with Professor Milnes Marshall at Owens College, returning again as Assistant Naturalist. In 1893, he was elected a Fellow of Lincoln College and to a Lectureship in 1894; so for a time returned to Oxford and was there when Ray Lankester was in the Linacre Chair. But in vacations he continued to work at Plymouth, and in these early years he wrote many papers on the morphology, bionomics and distribution of marine invertebrates. He was particularly attracted to the nudibranch molluscs and did pioneer experiments to test and confirm the hypothesis of their warning coloration. He began his researches on the Tunicata, the group to which he was to return in later life; and it was in this period too that he published his delightful studies on the habits and respiratory mechanisms of the sand-burrowing crabs. It was from Oxford in 1895 that he brought a batch of undergraduates to Plymouth to inaugurate the first of the series of Easter classes. In the pages of reminiscences I have referred to he gives the names of some of the students in these classes who later distinguished themselves in zoology; it is an interesting list.

His life's work may be divided into three periods: the first occupied with these many and various researches in pure marine biology; the second devoted to fishery investigations; and the third, when a university professor and in retirement, occupied with more fundamental problems in zoology and his poetic interpretations of bird song.

The second period began in 1897 when he went back once more to the staff at Plymouth; this time as Naturalist in charge of Fishery Investigations. He became the moving spirit in the development of fishery science in England. He was clearly much impressed by Johan Hjort's pioneering research in Norway, and his first paper in this period was an extensive account of Hjort's methods. Like Hjort he planned his work on a wide front and soon he was publishing papers on such different aspects of fisheries work as 'The Surface Drift of the English Channel and Neighbouring Seas during 1897', 'On Variation, Races and Migration of the Mackerel' (1898), 'On the Plankton and Physical Conditions of the English Channel' (1899) and on 'The Impoverishment of the Sea' (1900). Great things were astir in oceanography at the turn of the century; in 1899 the King of Sweden invited all the countries interested in the fisheries of the North Sea and adjacent waters to send representatives to Stockholm to a conference to discuss the possibilities of collaboration in a programme of marine research. A second conference was held, this time in Christiania (Oslo), in 1901, and Garstang went as a delegate of His Majesty's Government; this was the conference which set up the International Council for the Exploration of the Sea. Each country participating undertook to investigate a particular region of sea and different problems in fishery research so that, as time went on and their results came in, the whole area would be covered and all the bits of research fit together as part of one great plan. The different nations equipped their separate research vessels and marine laboratories.

The English and Scottish fishery departments were then, as still they are to-day, separate institutions; and the Fishery Board for Scotland had already begun its investigations well before the beginning of the century. The English department, a small branch of the Board of Trade as it was then, commissioned the Marine Biological Association to start its research for it as part of the international scheme; so it was that Garstang became Director of these investigations and established a laboratory at Lowestoft. With his assistants, William Wallace, R. A. Todd and George Atkinson, and the famous old research trawler *Huxley*, he carried out from Lowestoft those classical investigations into the natural history of the North Sea plaice which have laid the foundations of English fishery research. By extensive age determinations and measurements, and particularly by liberating vast numbers of marked fish at different points (to be returned when recaught by fishermen), he studied the natural growth-rates and migrations of the fish in different areas. He realized how overcrowded the young plaice were on the nursery grounds off the Dutch

coast and how much more food there would be available for their growth on the Dogger Bank; so he tried the experiment of transplantation. He caught and marked large numbers of young fish on the coastal banks; half of these he returned to the sea where he caught them and the rest he carried in tanks of sea water to be released on the Dogger Bank. When in time the marked fish were recaught it was found that those taken to the richer feeding grounds had in two years grown twice as big as those left behind. Garstang had pointed the way to a farming of the sea, but he was before his time. In his Buckland Lectures in 1929 he returned to the subject and showed how such a transplantation on a large commercial scale could be made to pay, the increased yield of fish giving an ample margin of profit over the estimated cost of transport; but no nation was likely to undertake the cost of this, for all other nations would be free to reap the reward. While the nations work together in the science of the sea, the days of their co-operation in its exploitation are still far in the future; but one day surely the North Sea will be farmed in the way that Garstang showed—let us hope that his name will then be remembered.

In all these early years he played a prominent part in the development of the International Council; from 1902 to 1908 he was scientific adviser to the British Delegates and convenor of the International Committee on Trawling Investigations. In 1906 he was awarded his Oxford D.Sc.

Garstang was an individualist, a lover of freedom and independence, who resented what appeared to him to be interference in his scientific programme when official government policy did not coincide with his own plans. At the same time as the newly constituted government Fishery Department decided in 1907 to take over the investigations from the Marine Biological Association he received a letter inviting him to accept the Chair of Zoology at the University of Leeds. It was a difficult decision for him to make; on the one hand he loved his marine work, on the other he felt he would never be happy if he was not entirely free to shape his own policy. Very reluctantly he resigned from his Directorship at Lowestoft, and on becoming Professor Garstang the third phase of his life began. In passing, it may be said that he regained a connexion with this work in 1919 when he was appointed a member of the Development Commission Advisory Committee on Fishery Research, on which he served till the end of the recent war.

For a time his output of research was much reduced. He had all his lectures to prepare; he was building an honours school of zoology where none had existed before; and he was making himself a terrestrial naturalist instead of a marine one. Insects and birds became the objects of his field studies. It was at this time that his love of nature and his strong poetic feeling led him to delight in the study of bird song which he later interpreted in verse and musical notation in a little book *Songs of the Birds* which went through several editions.

After nearly twenty years of marine work he came back to more academic zoology, and took up again the study of those problems which had fascinated him when he was an undergraduate at Oxford in the heyday of speculation as to the evolutionary origin of the different groups of animals. The main trends of zoological interest had in the meantime flowed into the fields of more experimental and genetical work; by the time he came to publish his morphological and embryological speculations, now into the 1920's, they were considered by many as out of date. Nevertheless in this, for the time being unfashionable field, he made contributions to his science of outstanding and lasting value. In his essay on 'The Theory of Recapitulation' which he read before the Linnean Society in 1921 (published in the Society's *Journal* the following year) and in his presidential address to Section D of the British Association in 1928 he put forward his revolutionary views on the influence of modifications in ontogeny upon the course of evolution. With them he helped to overthrow the influence of Haeckel's so-called 'Biogenetic Law' which had dominated zoological thought for so long. Garstang coined the term *paedomorphosis* to apply to the evolutionary influence of larval characters upon adult organization. In two large papers, 'The Morphology of the Tunicata, and its bearings on the Phylogeny of the Chordata' (*Quart. Journ. Micr. Sci.*, Vol. LXXII, pp. 51–187, 1928) and 'The Morphology and Relations of the Siphonophora' (*Ibid.*, Vol. LXXXVII, pp. 103–93, 1946), he showed how paedomorphosis, by a process of neoteny, appeared to have played a leading role in the evolution of both chordates and the siphonophores. The theoretical importance of these ideas is more fully dealt with in an obituary written for the *Proceedings of the Linnean Society*.

He was a great teacher, who by his infectious enthusiasm, filled his pupils with a love of zoology; he was also their friend. I cannot do better than quote from the obituary notice written in *Nature* by Professor L. Eastham, one of his former pupils:

> Few who go from us will leave behind so much affection and such a sense of gratitude. It is inevitable that his students will remember Garstang for his perpetual youth and his genial kindness. They will think of their visits with him to the marine station which he established at Robin Hood's Bay; of teas in the laboratory at which he and Mrs Garstang were generous hosts and at which the week's problems were discussed; and of their open house at Meanwood where all students were welcome.

There was yet that other important side of his personality; his strong poetic feeling which partly found expression, as already stated, in his studies of bird song, but in addition provided a large number of poems of which only a few were published. Among the latter I may mention: 'The Song of the Tree Pipit' (*The Times*, 8 May 1919); 'The Return to Oxford: a Memorial Lay' (a long poem published by Blackwell of Oxford in 1919) describing his thoughts on visiting Oxford just after the war, seeing the young men returning, and mourning the death of his zoologist friends and former companions at Oxford:

Geoffrey Smith, Wilfred Jenkinson, Arthur Darbishire, Edward Minchin and George Grosvenor; 'To a Herring Gull' (*The Oxford Magazine*, 6 February 1920) and 'Friendship' (*Nature* 7 July 1921). Then there were his essays 'Wordsworth's Interpretation of Nature' which was published as a special supplement to *Nature* (16 January 1926) and 'Wordsworth's Green Linnet' (*Nineteenth Century*, September 1929).

After his retirement, Oxford became the home of the Garstang family, and here he continued his researches and writing up to the very end. On his 81st birthday, and less than a fortnight before he died, he went up to London to take part in the special symposium on Bird Song at the Linnean Society. His very happy life and biological interests were shared by Miss Lucy Ackroyd, of Newnham College, whom he met at the Plymouth Laboratory and married in 1895; she died in 1942 and they are survived by a son and five daughters.

A. C. HARDY

OBSERVATIONS ON THE LIFE HISTORY AND FUNCTIONAL MORPHOLOGY OF *CERITHIOPSIS TUBERCULARIS* (MONTAGU) AND *TRIPHORA PERVERSA* (L.)

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(Text-figs. 1–6)

CONTENTS

	PAGE
Introduction	567
Cerithiopsis tubercularis (Montagu)	568
Triphora perversa (L.)	576
Discussion	580
Summary	585
References	586

Introduction

Cerithiopsis tubercularis occurs along the west and south-west coasts of the British Isles. It may be collected from intertidal coralline pools, especially those in which ample sponge growth occurs, or from the sheltered sponge-covered slopes and crevices of rocks, and under boulders, in the lower third of the intertidal zone. It is also dredged in Plymouth Sound and outside where, again, it is associated with sponges. *Triphora perversa* is found in a somewhat similar habitat; inshore, however, *Triphora* is confined to rock crevices and slopes within, or immediately above, the laminarian zone. In their internal anatomy these two prosobranchs have many points of resemblance, and they are placed in consecutive families of the order Mesogastropoda (Thiele, 1929). Both are of approximately the same size, the pointed tuberculate shell attaining a height of 8 mm. in *Triphora*, and 7·5 mm. in *Cerithiopsis*. The former, however, is sinistrally coiled, the latter dextrally: the organs of the mantle cavity of *Triphora* and also the nervous system are, in their arrangement, mirror images of those of the dextrally coiled *Cerithiopsis*. Their anatomy is little known: Fischer (1887) gives a drawing of the radula of *Triphora*, though this is incomplete, and more recently Risbec (1943) gives a brief description of some points in the gross anatomy of the proboscis, oesophagus and nervous system of *Triforis* (= *Triphora*) *montrouzieri*. Pelseneer (1926) describes the eggs and newly hatched larvae of *T. perversa* from the coast of Brittany, and Lebour (1933) describes and figures the external features of these larvae as

well as those of two species of *Cerithiopsis*—*C. tubercularis* and *C. barleei*. She is also the first to describe the egg masses of *C. barleei* (1933) and *C. tubercularis* (1936), which are embedded in the tissues of the sponges *Ficulina ficus* and *Hymeniacidon sanguinea* respectively.

Cerithiopsis tubercularis (Montagu)

Cerithiopsis tubercularis rests on the surface of sponges, adhering by means of the copious supply of mucus from the foot, or buried in their superficial tissues so that only half the length of the shell, or even less, is visible. The animals are reluctant to feed in captivity, and it is probably for this reason that the feeding mechanism has not been observed, and the correlated structures described. Specimens collected inshore from the south coast of Cornwall show a preference for *Hymeniacidon sanguinea*, and during the late spring and summer months, which is the breeding season, a number of mature individuals may be found on a single cluster of the sponge; in early August as many as twenty have been collected from 12 sq. in. of *Hymeniacidon*. The molluscs feed on the tissues of this sponge as well as laying their eggs therein, and they suck up the tissues through a comparatively long proboscis. The feeding mechanism, however, may be difficult to see. On the few occasions when it has been observed the proboscis has been thrust out of sight through an osculum or into the irregularities of the broken surface of the sponge.

A number of young, immature specimens, averaging 1·25 mm. long, have been found on the shells of *Chlamys opercularis* in dredgings from the Rame-Eddystone Ground. These were collected in early January, presumably developed from summer spawn. In the same dredgings mature individuals 5·5 mm. long were obtained, though not on the bivalves, nor would they, like the younger ones, exploit these shells for their food when given the opportunity. The young will collect diatoms and detritus from the narrow crevices of the shells by means of the proboscis, and if separated from the bivalve will quickly return to it. Although the adult shows a special liking for sponges it will perhaps take other food, for Lebour (1933) states that 'adults were kept for a month in plunger jars and lived quite happily without the sponges, probably feeding on debris or small algae'.

The foot, by which the mollusc keeps a firm hold whilst feeding and when washed by the waves of the ebbing or flowing tide, is truncated in front and tapers to a blunt point posteriorly. It is capable of considerable and rapid distention, and frequently a temporary transverse groove demarcates the anterior half, which is rectangular in shape and contains the opaque white tissues of the anterior pedal mucous gland, from the triangular posterior half with the posterior pedal gland and the operculum. The anterior gland opens by a transverse slit along the anterior margin of the foot and comprises not only mucous glands, but a second type of cell with discrete spherules of a different

type of protein filling the cytoplasm. The sole of the foot is covered by a ciliated columnar epithelium with numerous mucous cells and between the ciliated cells run ducts from sub-epithelial mucous glands. The posterior pedal gland, as in other prosobranchs of small size (Fretter, 1948), is too big to be accommodated wholly in the tissues of the foot and spreads into the haemocoel of the head where it lies anterior to, and alongside, the nerve ring. Its opening is near the middle of the sole, just within the posterior half, appearing sometimes in the form of a longitudinal slit, sometimes as a deep pit, and from it a transient, median, longitudinal groove conveys the secretion, augmented by mucus from the surface of the sole, to the posterior tip of the foot. This fluid may be used as a viscid climbing rope which allows the animal to lower itself from its inverted swimming position on the surface film of water in a rock pool, or it may be used to secure the animal on a wave-swept rock. The opening of the posterior gland leads dorsally into a ciliated duct which resembles histologically the surface of the sole, and as the duct passes inwards it bifurcates, branching to each side of the head. Each lateral branch receives two diverticula lined by tall mucous cells; no sub-epithelial glands occur.

The head bears a pair of long, linear tentacles, beset, especially around the distal half, with bristle-like motionless cilia, and as the animal moves along the tentacles are waved as though sensing the pathway. In the base of each is embedded an eye, surrounded by connective tissue and separated from the columnar epithelium by a sparse layer of muscles. No snout is developed, nor a mentum: from the anterior pedal mucous gland the dorsal surface of the foot curves upwards and backwards to the head which is concave in the transverse plane between the eyes, and in the centre of the concavity lies a small inconspicuous opening. This is the opening of the introvert (Fig. 1A, o) at the base of which the mouth (M) is placed.

The introvert is lined by columnar epithelium, slightly cuticularized and rich in mucous cells. Immediately beneath the epithelium is an intrinsic musculature of circular fibres and beneath this lie muscles which form part of the mechanism for the retraction of the proboscis. The retractors run parallel to the length of the introvert and buccal cavity from which they arise, and posteriorly they converge to form a compact, closely knit sheet (Fig. 1 A–C, R), which lies ventral to the oesophagus, alongside the columellar muscle, and so passes up the spiral of the shell to be inserted on the columella itself. Other muscles run from the gut wall directly on to the body wall, passing through the nerve ring when the proboscis is retracted. Of these many from the anterior wall of the introvert to the wall of the head are short (Fig. 1 A, D) and act as dilators, and of the longer ones three bundles are particularly conspicuous (PR)—from the head they traverse the whole length of the introvert and buccal cavity to their insertion on the wall of the anterior oesophagus, and will help in the extension of the proboscis, though this is chiefly brought about by pressure on the blood in the haemocoel exerted by the musculature of the body wall.

When the proboscis is fully everted the mouth (M) is carried to its tip and just within the buccal cavity a pair of horn-coloured jaws (J) may be visible dorsally and the tip of the odontophore (OD) ventrally. The jaws are close together, one on either side of the mid-dorsal line, and each is composed of forty or so long spikes packed tightly to form a semicircular pad. Each spike is secreted by a single epithelial cell and has an irregularly blunted tip. When

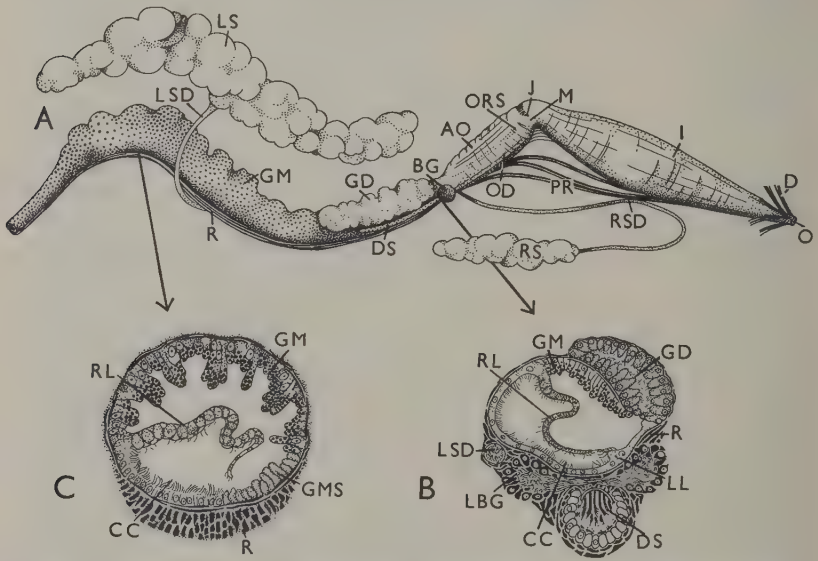

Fig. 1. *Cerithiopsis tubercularis*. A, anterior part of alimentary canal. × 40. B, transverse section at level indicated. × 240. C, transverse section at level indicated. × 170. AO, anterior limit of anterior oesophagus; BG, buccal ganglion; CC, ciliated channel; D, dilator muscles; DS, radular sac; GD, glandular diverticulum of oesophagus; GM, glandular wall of mid-oesophagus; GMS, second type of gland cell of mid-oesophagus; I, introvert; J, right jaw; LBG, left buccal ganglion; LL, left longitudinal fold; LS, left salivary gland; LSD, duct of left salivary gland; M, position of mouth; O, opening of introvert; OD, odontophore; ORS, opening of right salivary duct into buccal cavity; PR, protractor muscles of proboscis; R, retractor muscles of proboscis; RL, right longitudinal fold; RS, right salivary gland; RSD, duct of right salivary gland.

the mollusc is feeding, with the proboscis thrust through an osculum to get at the softer tissues of the sponge, the jaws loosen the tissues which are then raked up into the buccal cavity by the numerous fine radular teeth. The long median teeth of the radula (Fig. 2, M) are spoon-shaped with the free edge produced into a few long spike-like cusps; the teeth lateral to these bear more numerous and shorter cusps (L). The action of both jaws and radula is lubricated by the copious saliva from the salivary glands (Fig. 1 A, RS, LS) which open one behind each jaw (ORS).

The buccal cavity and the short anterior oesophagus (AO), which lies immediately behind the point where the radular sac separates from the rest of the gut (Graham, 1939), comprise a muscular tube, its posterior limit marked by the large, conspicuous buccal ganglia (BG), the size of which is correlated with the delicate manipulative power of the proboscis. Along the roof is a narrow dorsal food channel bordered by broad, muscular folds. In the buccal cavity the epithelium of the folds has no basement membrane and the intrinsic radial muscles which dilate the dorsal channel to suck in the food penetrate between the epithelial cells; interspersed with these muscles are occasional circular and longitudinal fibres. Posteriorly, in the region of the buccal ganglia, the bases of the longitudinal folds narrow, the left becoming inconspicuous, the right deep and glandular.

The two salivary glands (RS, LS), which appear as opaque white, lobular masses in the living state, are remarkably unequal in size, and their histology is also different. Each has a long, narrow, ciliated duct (RSD, LSD) which from its opening, posterior to the jaw (ORS), runs straight back through the wall of the buccal cavity and anterior oesophagus, and then, as a result of torsion, is twisted around the oesophagus. The right duct curves over the dorsal and then down the left wall of the anterior oesophagus immediately in front of the left buccal ganglion. It then lies freely in the haemocoel and describes, when the proboscis is retracted, a forwardly directed U-shaped bend, running forward as far as the nerve ring, bending ventralwards, and reversing its course to join the small salivary gland which lies ventral to the gut. When the proboscis is protruded the duct will be carried out into the introvert along the oesophagus. The right salivary gland is a simple tube and has only one type of secretory cell, which alternates with ciliated cells and produces mucus.

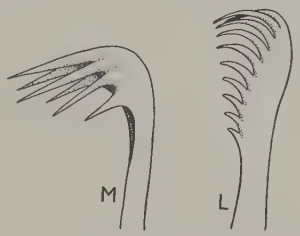

Fig. 2. *Cerithiopsis tubercularis*. Teeth of radula. ×3300. L, lateral tooth; M, median tooth.

The left salivary duct (Fig. 1 A, B, LSD) curves ventrally around the left wall of the oesophagus immediately behind the left buccal ganglion (Fig. 1 B, LBG), passes back through the thickness of the ventral retractor muscles (Fig. 1 A, R), and eventually, freed to the haemocoel, joins the central region of the relatively enormous left salivary gland (LS) which is displaced dorsally. The wall of this gland is deeply folded and, although ciliated cells alternate with gland cells in the main channels which open to the duct, it is difficult to trace ciliated cells in the finer ramifications of the gland. The secreting cells are of two types: some, the minority, produce mucus; the others are filled with small spherules which stain lightly with iron haematoxylin, whereas the surrounding cytoplasm is deep blue-black after this stain. Perhaps this second type of cell produces

an enzyme which is mixed with the tissues of the sponge as they are loosened.

The oesophagus is divisible into three regions: the anterior and posterior which are short, and the middle region (GM) which is long, glandular and has a continuation of the dorsal food channel (Fig. 1 B, C, CC). The right longitudinal fold from the buccal cavity and anterior oesophagus passes into the mid-oesophagus as a thin, deep sheet of tissue (RL) which stretches across the lumen to the opposite wall, and extends down the length of the mid-oesophagus separating the dorsal glandular section from the ventral ciliated area. The insignificant left fold is difficult to trace beyond the initial region of the mid-oesophagus (Fig. 1 B, LL). The first 90° of torsion occurs in the region of the buccal ganglia, and is an abrupt twist which brings the originally dorsal ciliated area on to the left side (CC), and the right longitudinal fold on to the dorsal wall (RL); to the right of this fold the wall of the oesophagus is glandular. The second 90° of torsion is more gradual and at its completion the glandular region comprises the dorsal and lateral walls; the smaller ciliated area is ventral.

If an animal be dissected the glandular area of the oesophagus is seen to be divisible into two regions: along the whole of its length the gland cells which form the dorsal and dorso-lateral epithelium of the mid-oesophagus are emerald green in colour (Fig. 1, GM) but, in contrast, there is anteriorly a mass of white glands against the right wall. This is a diverticulum (Fig. 1 A, B, GD) of mucous cells alternating with ciliated cells which opens at its anterior end to the anterior oesophagus beneath the small left longitudinal fold, and marks the posterior end of this part of the gut. The diverticulum is involved in the first 90° torsion of the gut so that its free end stretches back along the right wall of the oesophagus. A diverticulum in a corresponding position, though thin-walled and larger, is present in *Lamellaria perspicua* anterior to a large oesophageal pouch which has its secreting area increased by the development of deep septa. Behind it in *Cerithiopsis* there is no swollen pouch: the presence of such would be impracticable, for the mid-oesophagus must be narrow enough to pass through the confined space in the nerve ring when the proboscis is protruded. Thus, although an equivalent amount of secreting area is developed in *Cerithiopsis*, it is not concentrated, but spread along the elongated section of the oesophageal tube, covering three-quarters of the wall. In *Lamellaria* and in *Trivia arctica* and *T. monacha* the right longitudinal fold which borders the dorsal food channel and passes back from the buccal cavity to the oesophagus, is deeper than the left. This discrepancy is much more pronounced in *Cerithiopsis* (Fig. 1 B, C, RL), where the right fold partitions off the glandular area from the ciliated channel (CC), acting, perhaps, as a valve to prevent the suction of the secretion from the oesophageal glands into the proboscis when it is extended. The fold gradually tapers away towards the posterior end of the mid-oesophagus. It is formed of a fold of epithelium with very little connective

tissue between the two layers of cells. On one side, that facing the ciliated channel, the epithelium consists of large mucous cells and wedge-shaped ciliated cells between them; on the other side the cells are flattened and bear no cilia.

The common type of gland cell, which is filled with green spherules in the living tissue, is little affected by acid fixatives; with iron haematoxylin the spherules stain lightly and with azan they stain blue. Between these glands and the ciliated cells on the post-torsional right side of the mid-oesophagus, that is, facing the free edge of the longitudinal septum, is a longitudinal strip of another type of epithelial gland (Fig. 1 C, GMS) in which the cytoplasm is filled with globular secretion masses, colourless during life, dissolving readily in acid fixatives. The cytoplasm of these cells stains deeply with iron haematoxylin and red with azan.

The short posterior oesophagus is ciliated throughout; the tube is narrow, of capillary dimensions, and runs straight back immediately above the columellar muscle to open into the antero-ventral wall of the stomach which is a small bag receiving two ducts from the digestive gland—one ventral and not far behind the oesophageal opening, the other dorsal and not far behind the antero-dorsal intestinal opening. The stomach is lined by an epithelium on which the cilia are densely packed and in no part is there a cuticular covering; the musculature is rather poorly developed. After a meal the lumen may be filled with the tissues of *Hymeniacidon* including long monaxon spicules, and nothing but a sheet of mucus shields the gastric wall. This general simplification of structure, in which the stomach is little more than a crop in which the meal lies to undergo digestion and from which the products of digestion are passed to the digestive gland, is paralleled in dorids which have adopted a similar diet. Throughout the gastropods such simplification is mainly correlated with the development of a macrophagous carnivorous habit and extracellular digestive processes (Graham, 1949).

From its origin the intestine passes dorsally over the kidney and forwards along the right side of the mantle cavity to the anus, which lies well within this cavity. It is ciliated throughout. The middle region is distinguished histologically by the large number of gland cells scattered amongst the ciliated cells. Each is filled with colourless spherules which respond readily to stains for protein, and when discharged the secretion droplet swells giving an irregular and indistinct outline, and presumably helps to elaborate the faecal rod around which the secretion can be traced. The rod contains not only sponge spicules but orange concretions pigmented like the sponge on which the mollusc feeds and similar to the concretions in the faeces of *Diodora apertura*, which also feeds on *Hymeniacidon*. Three types of cell occur in the tubules of the digestive gland: two are rather infrequent and confined to the crypts; elsewhere the digestive cell occurs. Fluid contents from the stomach and extremely minute particles of food can be traced to the vacuoles of the digestive cell, where

presumably digestion is completed. These vacuoles may occupy a half or two-thirds of the cytoplasm, whilst below them are tightly packed spherules. In a starved individual the spherules fill the entire cell, and sections of an individual which was interrupted at the commencement of a meal suggest that they are secretory: they can be traced into the tubules of the gland and into the ducts where they swell and their identity is ultimately lost. The cells in the crypts of the tubules are highly vacuolated throughout, and the vacuoles contain spherules. In one type of cell, the more numerous, the spherules, apparently colourless at first, may change in consistency and coalesce into brown masses which have the appearance of excretory matter. The second type of cell contains lime spherules.

In *Cerithiopsis* the sexes are separate and in both male and female the glandular pallial section of the genital duct is open along its length to the mantle cavity. As in other mesogastropods in which this duct is open—*Turritella communis* (Fretter, 1946), *Bittium reticulatum* and *Scala communis* (Johansson, 1947)—no penis is present. The transference of sperm to the female was once observed during August when ten individuals, together with the piece of *Hymeniacidon* on which they were found, were kept under observation. The molluscs were clustered together, and from the males sperm mixed with prostatic secretion left the mantle cavity in the exhalant stream and clouded the surrounding water. Little dispersal of the sperm occurred, however, for immediately the fluid was sucked through the short inhalant siphons of the adjacent females—the ultimate destination of the sperm was traced in sections.

In the testis both eupyrene and apyrene spermatozoa are developed and are stored in the large vesicula seminalis which constitutes the initial part of the vas deferens. The apyrene sperm have not been traced farther forwards in the duct, nor have they been seen in the female. From the vesicula seminalis a short vas deferens, closed by a sphincter except during copulation, passes forwards over the columellar muscle on the right side of the visceral mass and opens to the prostate, the pallial vas deferens, which lies along the junction of body wall with mantle skirt on the right side. The prostate has deep lateral walls joined by a narrow dorsal wall, and is open ventrally. Its epithelium consists of tall gland cells alternating with ciliated cells: proximally the glands respond to stains specific for mucus, whilst anteriorly, throughout the greater length of the duct, only an occasional cell secretes mucus, and there is a second type of gland in which the cytoplasm is uniformly vacuolated and the vacuoles contain spherules staining lightly with iron haematoxylin. The pallial duct extends along the mantle cavity as far as the level of the anus.

The disposition of the female genital duct is similar to that of the male. From the ovary a short ovarian duct, with an epithelium similar to that of the gonad, passes forwards along the right side of the visceral mass, just above the columellar muscle, to the renal oviduct. This is short and ciliated, leading to

the postero-ventral limit of the pallial duct. The pallial duct is better developed than the homologous region, the prostate, in the male, though, like it, it has deep lateral walls joined by a narrow dorsal wall, and, except at the extreme posterior end where there is a small cul-de-sac, it is open along its ventral edge. The cul-de-sac receives ventrally the renal oviduct and dorsally it accommodates spermatozoa received from the male by way of the inhalant water current. If a female be fixed immediately after taking up a supply of spermatozoa, sections

Fig. 3. *Cerithiopsis tubercularis*. Part of a transverse section through a receptaculum seminis. ×357. CE, columnar epithelium surrounding entrance to receptaculum; DR, duct leading to receptaculum; G, gland cells; N, nucleus; S, orientated spermatozoa; SE, spermatozoa in vacuoles of epithelial cells.

show that many of the sperm are concentrated in a limited region of the pallial duct, along the dorsal wall, at the entrance to the cul-de-sac. Here there is a small, shallow pouch, lined only by ciliated cells, where the sperm may be orientated. Still other spermatozoa have travelled up a muscular and ciliated duct which leads dorsally from this pouch and bifurcates at its distal end. Each bifurcation (Fig. 3, DR) opens to a receptaculum, the two receptacula lying one above the other on the right side of the rectum. They are approximately spherical sacs lined, except around the entrance, by relatively enormous cells (G) in which the long nuclei (N), each with a number of nucleoli, may be twisted into a variety of shapes. The cytoplasm of these cells is vacuolated and contains spherules which dissolve in acid fixatives. Around the entrance to the receptaculum is a circular patch of low, columnar epithelium (CE) and in its distal cytoplasm the heads of spermatozoa (S) are embedded. Not all the sperm

are thus accommodated: others lie in tangled balls in vacuoles of the giant epithelial cells (SE) and here they appear to undergo digestion.

The gland cells of the pallial duct alternate with ciliated cells and are especially tall in the lateral walls. The cul-de-sac has mucous cells only. Anteriorly, the spherules which fill the secreting cells are of uniform size and are colourless in living tissue: near the cul-de-sac they respond slightly to mucicarmine and celestine blue; elsewhere they stain lightly with iron haematoxylin and the cytoplasm in which they are embedded stains deeply. These anterior glands produce a colourless fibrillar secretion which forms the resistant coat of the egg capsule, the posterior part of the pallial duct giving the albumen in which the eggs are embedded.

At the level of the anus the gland cells of the pallial duct are replaced by ciliated cells, and the duct is reduced in diameter. It extends beyond the anus as a shallow, ciliated groove leading towards the mouth of the mantle cavity, and ends a short distance from this opening.

Within the mantle cavity alongside the posterior third of the pallial duct and extending back to the kidney aperture is a ventral gutter which is lined by mucous glands and cells with exceptionally long cilia. It runs between the body wall and the median wall of the oviduct, providing a pathway by which sperm are directed first to the proximal part of the pallial oviduct and then to the receptaculum. It has no homologue in the male.

TRIPHORA PERVERSA (L.)

Triphora perversa is the only British member of the family Triphoridae and consequently the only British mesogastropod which is typically sinistrally coiled. This direction of coiling, determined by a reversal of the normal cleavage pattern, brings about a reversal of the arrangement of the organs in the mantle cavity: the osphradium and ctenidium are on the right side, which receives the inhalant stream of water by way of a short siphon, and the rectum and genital duct are on the left. The visceral loop of the nervous system shows, moreover, that the direction of torsion is also reversed, for the left pleuro-visceral connective with its parietal ganglion is supra-oesophageal. The ganglion is thus close to the osphradium which it innervates, and the right connective runs ventral to the gut bringing the right parietal ganglion beneath the oesophagus. The pleuro-parietal connectives are short as in the Cerithiidae, concentrating the parietal ganglia in the head. The visceral ganglia, however, lie posteriorly, near the stomach, and their long fine connectives with the parietals, lengthened on account of the development of the introvert, are difficult to trace.

When the animal is crawling the exposed parts of the body, opaque white in colour, can be seen to resemble those of *Cerithiopsis*, and this resemblance extends to feeding habits as well.

Specimens of *Triphora perversa* collected from the laminarian zone of south Cornwall have frequently large numbers of monaxon, siliceous sponge spicules in their stomachs, and with these diatoms may occur. In captivity, the animals rarely feed though supplied with fresh *Hymeniacidon* and *Halichondria*—the sponges with which they are associated on the shore and in the substance of which the shell may be partly or completely hidden. On two occasions only has the protrusion of the proboscis been observed; on one of these tissues of *Halichondria panicea* were sucked into the gut. The proboscis was thrust out of sight through an osculum of the sponge, seeking presumably the softer tissues. The surface of the proboscis is covered by an epithelium containing two types of glands: the more numerous is a mucous cell; in the second the secretion appears as minute discrete granules which are colourless in the living tissue and

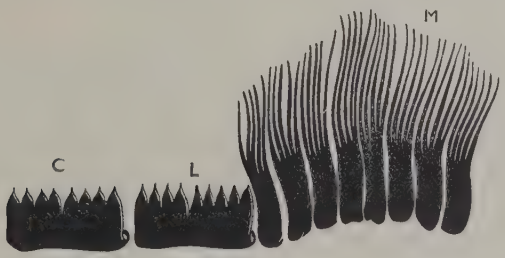

Fig. 4. *Triphora perversa*. Half row of radular teeth. × 1700. C, central tooth; L, lateral tooth; M, marginal tooth.

so numerous that they obscure the large basal nucleus. The epithelium is surrounded by its intrinsic layer of circular muscle fibres and external to these are the muscles of the proboscis which run back to their insertion on the columella.

When the proboscis is fully everted a pair of dorso-lateral jaws is brought to its tip, and ventral to them lie the teeth of the radula. The jaws form two large triangular plates which surround the buccal cavity anterior to the odontophore, the broad bases of the triangles meeting mid-dorsally. Their blunt spikes, each comprising the secretion from a single cell and providing a flattened plate slightly raised in the centre, are firmly sutured together, the sutures being slightly wavy. The superficial appearance of these jaws is reminiscent of the jaws of a skate. The radula consists of numerous rows of minute teeth. In each row the single central tooth (Fig. 4, C), attaining 10μ broad and 5μ high, has eight equal cusps, short and broad, and arranged in two groups which are separated from one another by a fissure. This tooth is bordered on each side by a single lateral (L) differing from it only in the number of cusps, nine, and these are again arranged in two groups separated by a fissure; the number of

lateral cusps varies from five to six, and in the median group there are either four or three. The numerous marginal teeth (M) are each about one-third the breadth of the central or lateral, and the longest may attain four times the height; the distal end is frayed out into fine pliable processes which sweep into the buccal cavity the tissues loosened by the jaws and by the biting teeth of the radula. Dorsal to the odontophore the buccal cavity is cuticularized.

Within the extended proboscis is the narrow, muscular oesophagus, which passes back from the buccal cavity, and the large salivary glands. The saliva is poured into the oesophagus, not far from its origin, by a single glandular duct which is divided histologically into two regions and is formed by the union of two short ducts from a pair of glands. These glands are enormous and unequal in size; when the proboscis is retracted the larger extends anteriorly as far as the nerve ring and posteriorly as far as the stomach; the smaller lies wholly behind the introvert, mainly ventral to the oesophageal tube and to the larger gland. It is a simple tubular gland, whereas the walls of the dorsal one are folded and its lumen insignificant. Three types of secreting cells occur in the salivary glands, and all of them are large with conspicuous nuclei. In both glands there are mucous cells, relatively more numerous in the ventral one, where they comprise more than half the epithelium. In the dorsal gland there is a second type of cell with spherules of irregular shape and size which stain with mucicarmine and also, deeply, with iron haematoxylin: the abundance of this kind of cell would appear to vary, for it may comprise about half the gland or only a small fraction; the frequency is inversely proportional to the third type of secreting cell which, although of constant occurrence and abundance in the ventral salivary gland, may be exceedingly infrequent in the dorsal. In this third type the cytoplasm is filled with spherules of uniform size which stain lightly with iron haematoxylin; the cytoplasm stains even lighter. A few of these cells may be found in the initial region of the duct from each gland, scattered amongst the mucous cells which comprise most of the epithelium. Along each duct, however, is a longitudinal strip of low cubical cells and after the ducts have united this non-glandular tract persists for a while together with the mucous epithelium. About half-way along its course the duct broadens and there is an abrupt histological change, and for the rest of its course—to its junction with the oesophagus—the most common type of cell is one filled with protein spherules which are not mucous and are unlike any in the gland. This cell makes up the whole of the secretory epithelium, except for a narrow longitudinal strip of mucous cells which continues to the oesophagus.

When the proboscis is withdrawn into the haemocoel, it passes through the confines of the nerve ring, which necessarily restricts its diameter, and comes to lie in the first two coils of the tightly spiralled shell: the mouth is now at its base; the long connectives between the cerebral and large buccal ganglia are directed posteriorly, the ganglia lying between the anterior end of the oesophagus and the ventral radular sac; the oesophagus is thrown into deep coils.

The oesophagus is a narrow muscular tube of uniform structure throughout the greater part of its length, surrounded by the retractor muscles of the proboscis. It is lined by a ciliated, columnar epithelium with only an occasional mucous cell; no dorsal folds can be traced along its length revealing the position of torsion. In *Triphora* the glandular areas are separated from the oesophageal tube. Not far from the stomach a pouch lies over the oesophagus and communicates with it dorsally at its posterior end (Fig. 5, GP). The dorsal and lateral epithelia of the pouch are thrown into numerous, deep, transverse folds (TF) which subdivide the lumen; radial muscles penetrate the folds and circular muscles form a thin outer coat. The epithelial cells are all secretory and they are of small size; the majority of the cells are filled with spherules which give

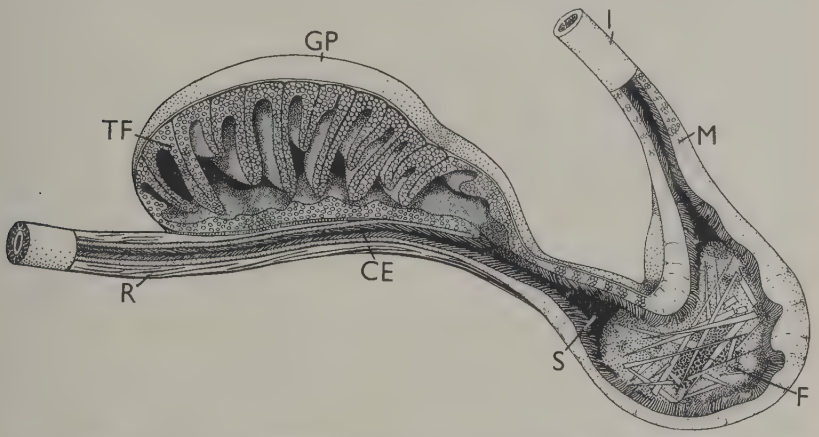

Fig. 5. *Triphora perversa*. Diagrammatic longitudinal section through the posterior oesophageal region, stomach and part of the intestine. × 140. CE, ciliated epithelium of oesophagus; F, food in stomach; GP, glandular pouch; I, intestine; M, mucous cells of mid-intestine; R, retractor muscle of proboscis; S, stomach; TF, transverse folds of epithelium.

the gland a yellowish appearance in the living state and are resistant to acid fixatives. With iron haematoxylin the spherules may all stain lightly, or some very deeply, and this difference in staining would appear to indicate stages in the elaboration of the final secretion—the lightly staining spherules being the precursors of the deeply staining ones. A considerable number of mucous cells also occurs in the epithelium; this is contrary to the typical condition in the lateral glandular pouches of the mid-oesophagus of gastropods for their function is to secrete enzymes, and only on rare occasions do they possess even a few cells secreting mucus or other lubricants (Graham, 1941).

At the posterior end of the oesophagus, between the opening of the gland and the stomach, the epithelium has exceptionally long cilia which direct a current posteriorly; along the dorsal wall are numerous mucous cells.

The plan of the rest of the digestive system is similar to that of *Cerithiopsis*: the stomach (S), a simple ciliated sac receiving anteriorly the opening of the oesophagus and above that the opening of the intestine; the intestine (I), a practically straight tube which leads over the kidney to the mantle cavity where, however, it runs along the *left* side to open towards the anterior end. The main duct from the digestive gland opens to the posterior wall of the stomach and anteriorly there is a small lobe of the gland which opens behind the opening of the intestine. The epithelium of the gland consists of tall club-shaped digestive cells, and excretory cells confined to the crypts of the tubules. The cytoplasm of the digestive cell is always vacuolated, although the details of its appearance depend upon the exact physiological state in which it is examined. In a starved individual the vacuoles appear to contain a uniform type of spherule, homogeneous in consistency and presumably containing a zymogen. There is only slight evidence that these are secretory for I have seen a few spherules freed into the lumen of the gland only on rare occasions. Sometime after a meal the distal ends of many of the digestive cells contain food vacuoles with ingested matter, fluid and minutely particulate; and much later yellow spherules, which can be traced to the faeces, occur in the same position. The stomach frequently contains numerous siliceous sponge spicules (F), and these appear to constitute the greater bulk of the faecal pellets; they are wrapped around with mucus which is secreted in large quantities from the epithelium of the mid-intestine (M).

The reproductive system in both sexes of *Triphora perversa* has an open pallial duct without sub-epithelial glands, and in the male there is no penis. It may be assumed from their close similarity in structure that the functioning of these ducts is similar to that of *Cerithiopsis*. There is, however, a difference in the receptaculum seminis which in *Triphora*, although lined by gland cells, shows no evidence of sperm absorption.

Discussion

Amongst the carnivorous gastropods there are several which browse on the tissues of sponges: *Diodora apertura* and some dorids may live exclusively on siliceous forms, rasping the surface tissues and taking relatively large mouthfuls into the gut. *Cerithiopsis tubercularis* and *Triphora perversa* are also sponge feeders, but they have adopted a different feeding habit. The acrembolic proboscis characteristic of many families of the mesogastropods has been lengthened in these two small animals so that it is long enough to pass through an osculum and reach the inner tissues of the sponge. In this way the spicular cortex which protects the sponge externally is avoided, and the softer parts sucked into the oesophagus; nevertheless, some spicules are taken up. The development of a long proboscis demands some modifications of the anterior part of the gut since this must move forwards through the narrow gap in the

nerve ring when the animal is about to feed and be withdrawn later. This involves an increase in length and a removal of projections which might obstruct its movement.

The oesophagus of the primitive gastropod is divisible into three regions: the anterior oesophagus which begins at the point where the radular sac separates from the gut; the mid-oesophagus with the dorsal food channel along its roof, and on each side a glandular region from which digestive enzymes are secreted; and behind this the posterior oesophagus. In this original condition the mid-oesophagus is swollen. The oesophageal glands are lost in some mesogastropods and the diameter of the tube then becomes uniform. This, however, occurs mainly in herbivorous forms, especially those with a constant stream of food into the gut, and the pouches are then replaced by a crystalline style in the stomach producing an amylase. In carnivores (Graham, 1939) where the next meal is unpredictable, the extracellular enzymes are better supplied by a gland under nervous control than by an automatic crystalline style; moreover, the demand is much more likely to be for a free proteolytic enzyme. In *Cerithiopsis tubercularis* the modifications of this region are met by the modification of the mid-oesophagus which is lengthened, with a consequent narrowing of its total diameter, and the glands are no longer concentrated in lateral areas as in the primitive prosobranch, but spread along the morphologically ventral and lateral walls; all trace of their paired origin is lost. The ciliated food channel covers the remaining wall and is separated from the glands by a longitudinal septum: this is the right dorsal fold which originates in the buccal cavity, bordering the dorsal channel, and remains normal in size until it reaches the posterior end of the anterior oesophagus when it rapidly enlarges and extends across the lumen to reach the opposite wall, even when the oesophagus is dilated. It not only provides mucus to lubricate the ciliated food channel where mucous cells are lacking, but also acts as a valve to prevent the sucking forwards of secretion from the oesophageal glands when the proboscis is extended during feeding.

The mid-oesophagus is, in all prosobranchs, involved in torsion; in *Cerithiopsis* this twisting of the gut includes also the posterior end of the anterior oesophagus. Into this posterior end opens a mucous pouch, attached ventrolaterally, but rotated on to the right side. There is no evidence that food is taken into the pouch: its epithelium is tall and glandular and the lumen relatively small; its opening beneath the small left dorsal fold may be covered by the free edge of the right fold. A ventral diverticulum from the oesophagus, immediately anterior to the oesophageal gland, is described by Amaudrut (1898) in *Cypraea arabica* and occurs in *Lamellaria perspicua*; in these molluscs, however, the diverticulum is larger, thin-walled and not differentiated histologically from the surrounding tissue: it may merely provide extra space in the oesophagus. The diverticulum in *Cerithiopsis* secretes a lubricant to augment the secretion from the right dorsal fold; the left fold has no mucous cells and cannot be traced beyond the anterior oesophagus.

The modifications in the oesophagus in *Triphora perversa* are more difficult to interpret. This region of the gut shows several anomalies: it consists of a muscular and ciliated tube which is elongated so that it must be looped within the haemocoel when the proboscis is withdrawn; it receives anteriorly the secretion from the salivary glands by a median glandular duct which is divided histologically into a proximal and distal part; the gland which opens into its dorsal wall posteriorly has a secreting epithelium which differs from that of the typical oesophageal glands in that it includes an appreciable number of mucous cells. From the structure of the oesophagus it is impossible to deduce the site of torsion. The fusion of the two ducts of the salivary glands to a single broad channel where, in the distal part, the common type of secreting cell is unlike any in the glands, and the fact that they discharge into the oesophagus,

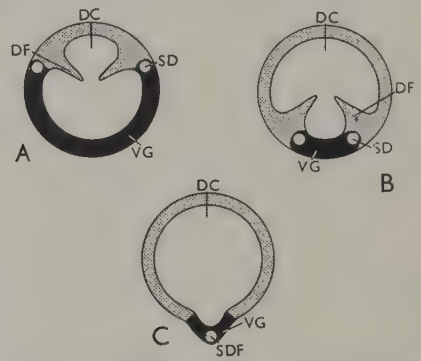

Fig. 6. A–C. Diagrams to illustrate the suggested relations of the dorsal food channel, ventral glandular region of the oesophagus and salivary ducts described on p. 578. DC, dorsal channel; DF, dorsal fold; SD, salivary duct; SDF, fused salivary ducts; VG, ventral glandular part of mid-oesophagus.

are, it would seem, conditions unparalleled in the gastropods. Typically, as in *Cerithiopsis*, the salivary ducts open into the buccal cavity, one on the outer side of each dorsal fold, and they (Fig. 6A, SD) may run back through the connective tissue of the anterior oesophagus along the base of the folds (DF) before passing to the haemocoel. Now the dorsal channel (DC) may be expanded and the ventral glandular part (VG) of the mid-oesophagus correspondingly reduced by the dorsal folds migrating ventrally (Fig. 6B), as has happened for example in the Stenoglossa (Graham, 1941), and when this takes place the salivary ducts (SD) migrate with them so that they come to lie side by side under the reduced ventral part of the oesophagus (VG). They may eventually fuse with one another and by losing their anterior sections open into the oesophagus here instead of into the buccal cavity (Fig. 6C). Now suppose that the ventral glandular part of the oesophagus, into which the single median salivary duct

now opens, is stripped off the remainder of the oesophagus from the anterior end backwards, then the conditions which obtain in *Triphora perversa* have been accurately reproduced—the oesophageal tube representing the dorsal food channel, the median glandular duct the oesophageal gland which has fused along its length with the proximal end of the salivary duct so that this opens into its posterior part, the line of fusion being represented by a longitudinal strip of mucous cells.

This interpretation of the oesophagus of *Triphora* does not account for the presence of a posterior dorsal gland which is constricted from the oesophagus not far from its junction with the stomach. The gland may represent a novel structure. That the oesophagus of the gastropod does give rise to such new parts is evident in the Buccinacea, the only family of the Stenoglossa with a dorsal caecum on the posterior oesophagus. The gland in *Triphora* agrees with this caecum in position, in the deep folding of its walls, and in possessing a number of goblet cells; but it differs from it in having an epithelium which, except for mucous cells, is histologically distinct from any other in the oesophagus. Brock (1936) suggests that the caecum in *Buccinum undatum* is merely an enlargement of the oesophagus to provide extra accommodation, and food with digestive enzymes enter it from the oesophagus; in *Triphora* there is no evidence that food is taken into the gland.

An open pallial genital duct in both sexes is known to occur in a number of families of the mesogastropods (Johansson, 1947) and is associated with the absence of a penis. It was described in *Turritella communis* (Fretter, 1946), a ciliary feeder living in a muddy situation, and was thought to be associated with the precautions which prevent excessive sediment entering the mantle cavity. To account for the open duct in such forms as *Bittium reticulatum*, *Scala communis* (= *Clathrus clathrus*) (Johansson, 1947), *Cerithiopsis tubercularis* and *Triphora perversa* seems perhaps at first sight more difficult; it is undoubtedly secondary and presumably advantageous.

It is well known that the mantle cavity of gastropods has to subserve a variety of functions mainly effected by a stream of water through it. In gastropods with a helicoid spiral shell the shape of this cavity varies considerably and is reflected in the form of the shell. This may be a close spiral with a small apical angle (e.g. *Cerithiopsis* and *Triphora*) or a rapidly expanding spiral with a large apical angle (e.g. *Lamellaria*); in the former case the mantle cavity is narrow and deep, in the latter broad and comparatively shallow. In the second group of gastropods the swelling of the pallial oviduct in the female, which occurs during the breeding season, and the presence of the penis in the male with its insertion into the pallial oviduct during copulation, would not interfere with the efficient functioning of the mantle cavity—in fact in viviparous forms like *Littorina saxatilis* there is sufficient space for the pallial oviduct to form a brood pouch accommodating a large number of embryos. The deep mantle cavity of *Turritella*, *Bittium*, *Cerithiopsis*, *Triphora* and *Clathrus*, which contains

a large gill following the course of the tight spiral of the shell, may have reached the minimal breadth for maintaining a proper ventilation of the whole cavity, and should it be still further restricted by the presence of a penis or a swelling genital duct its breadth might be brought below the limit for efficiency. Perhaps it is for this reason that the penis is lost and the sperm transferred to the female by a method involving an open pallial duct; moreover, in these molluscs the duct is long and thin without sub-epithelial gland cells. To test this hypothesis the examination of the shells of a series of mesogastropods was made.

The general appearance of a helicoid spiral shell depends upon (i) the angle of the equiangular spiral α, and (ii) the angle β which a tangent to the whorls makes with the axis of the shell—the half apical angle (Thompson, 1942).

TABLE I

Species with an open pallial genital duct in both sexes	No. examined	Average value for β
Turritella communis	10	8·5°
Bittium reticulatum	5	5·25°
Cerithiopsis tubercularis	6	3·25°
Triphora perversa	5	5·5°
Clathrus clathrus	8	7·5°
Species with a closed pallial genital duct in both sexes		
Littorina littorea	12	40·6°
Littorina saxatilis	12	39·0°
Rissoa parva	8	16·0°
Natica poliana	6	47·3°

These two values may change with age. A mean low value for the half apical angle β indicates a tall spire which, with tightly packed whorls, would have a high value for the spiral angle α, as in *Tenebra triseriata* where the spiral angle is 89·2° (Moore, 1936); on a flattened shell it would be impossible to pack the whorls so tightly. A flattened spire has a high value of β, e.g. *Velutina*, *Lamellaria* and *Planorbis*, the extreme case being in the pulmonate with a half apical angle of 90°; the two members of the Lamellariidae have a lower value of α, for their shells are rapidly expanding spirals. The difference in the magnitude of the spiral angle of such diverse shells as *Turritella* and *Natica* may only be 2° (Thompson, 1942), and since such a very small change in α may be associated with such disparity in shape it is clear that it is upon the angle β that the difference in their form mainly depends. Consequently, β is taken as the value of importance in the present consideration, and has been measured as the angle between the tangent to the last two whorls of the shell of mature individuals and the axis of the shell. The last two whorls were selected as they enclose the mantle cavity (Table I).

In all the British mesogastropods in which an open genital duct has been described in both sexes and there is no penis, β does not on the average exceed

8·5°, and in these species the mouth of the shell is small, about one-fifth of the height or less; the ctenidium is well developed and occupies a large part of the mantle cavity. In such tightly coiled spirals there will be a greater degree of shortening of the right side of the body and so less space for the right half of the pallial complex, which is, in the mesogastropod, the genital duct and rectum.

In some other mesogastropods the penis is lost and the pallial genital duct is open at least in one sex. From the description of a female *Cerithium telescopium* by Berkeley & Hoffman (1835) one may conclude that the pallial duct is open; the shell of this species is tightly coiled, with a small value for β (11·5°) and a very restricted opening. The pallial duct is also open in *Fagotia esperi* (Soós, 1936), in the male of *Cerithium vulgatum* (Johansson, 1947) and in the female of *Melanopsis dufourei* (Sunderbrink, 1929), but in these the body whorl of the shell is deep, though compressed, and its opening long, suggesting the presence of a more spacious mantle cavity. It may be that the specialized condition in these three molluscs is to be related to some unknown factor in their mode of life rather than to the shape of the shell. An alteration in shell shape may be recent and the structure of the genital duct not yet changed from the ancestral condition to conform to the new type of shell.

Summary

Cerithiopsis tubercularis and *Triphora perversa* feed on siliceous sponges: a long proboscis is thrust through an osculum of the sponge, or into breaks in the surface, to reach the softer parts. These are loosened by jaws, entangled in saliva and swept into the buccal cavity by the radula.

The formation of a long introvert, which must be withdrawn through the narrow space in the nerve ring and narrow enough to go through an osculum, has brought about (i) a lengthening of the mid-oesophagus in *Cerithiopsis*, with a narrowing of its diameter, and a spreading of the oesophageal glands along its length, (ii) in *Triphora*, a reduction of the ventral glandular part of the mid-oesophagus, its stripping from the food channel and a displacement of the salivary ducts so that they open into the glandular part of the oesophagus. In *Triphora* there is a dorsal gland of unknown function on the posterior oesophagus.

The stomach in both species is a simple ciliated sac: the oesophagus opens anteriorly and ventrally, and the intestine originates above this opening; there are two ducts from the digestive gland.

The pallial region of the male and female genital duct is open; and there is no penis. It is suggested that the open condition of the duct and the absence of a penis in the mesogastropods is correlated with a long, narrow mantle cavity which contains a relatively large ctenidium.

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STUDIES OF WATER MOVEMENTS AND WINDS AT VARIOUS LIGHTVESSELS

II. AT THE SEVEN STONES LIGHTVESSEL NEAR THE SCILLY ISLES

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(Plates I–IV and Text-figs. 1–9)

[This paper is published with the approval of the Lords Commissioners of the Admiralty, but the responsibility for any statements of fact or opinions expressed rests solely with the authors.]

Introduction

The purpose of this paper is to review the results obtained from a programme of continuous current measuring at the Seven Stones Lightvessel which lasted for upwards of 600 days. It is expected that the actual records amassed during that considerable period will be published in due course. For the present, reviews such as this are being prepared and published *seriatim* in advance of any major presentation of the detailed data.

This present paper follows shortly upon an earlier one, the subject matter of which was information entirely comparable in nature but very much less in extent. The briefer paper (Carruthers & Lawford, 1950) dealt with the water movements past the Mouse Lightvessel in the Thames Estuary, and is no. 1 in the series.

Marine biologists in general, and fishery research scientists in particular, attach importance to schemes of investigation which produce solid information on water movements adequate in time span to serve studies of the dispersal of passively drifting marine organisms. Because of this, there had come into being, by the time World War II broke out, a wide scheme of observations which aimed at amassing simple data on water flow past an ever-increasing number of lightvessels. The aim was to learn for all days of whole years (without intermissions imposed by bad weather) how a thick surface layer of water had moved at a sufficient number of places in the southern North Sea and the English Channel to produce a synoptic picture of value to workers

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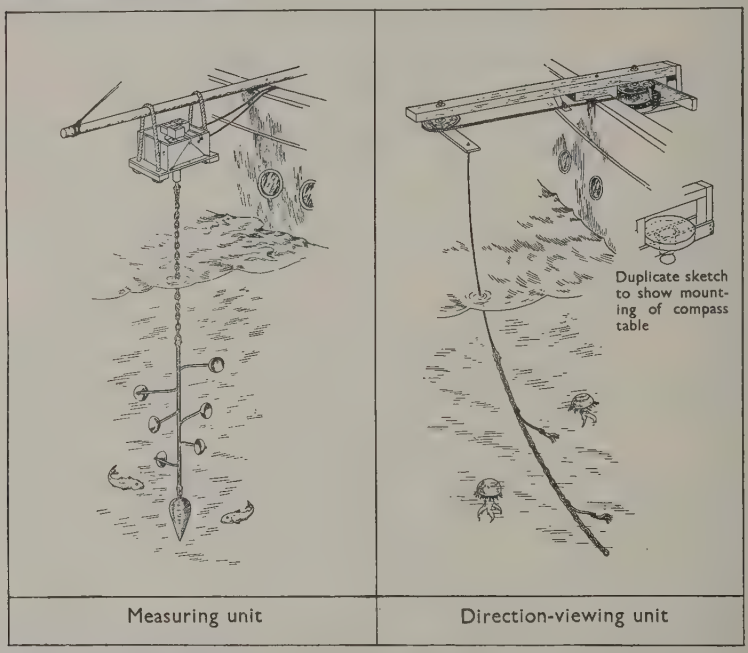
concerned with the life histories of fish and other organisms. The information gathered had real interest for others besides, such as engineers concerned with coast erosion, and seamen.



Text-fig. 1. The vertical log current meter as used aboard lightvessels. With this extremely robust (but not in this form automatic) instrument, a very large body of data on water-flow past lightvessels has been amassed. The observations have been carried on without any intermissions imposed by wild weather, and, throughout the entire winter of 1938–39, 'non-stop' observations were made with this instrument from ten lightships (English, French, Dutch and Danish) in the southern North Sea and English Channel... and also from the Seven Stones lightship near Land's End. A modified form of the instrument can provide for automatic observations from anchored ships, and a special version of it now exists for use from an unattended buoy so that the immobilization of an observing vessel is avoided. The resulting data on water movements are directly applicable to navigational needs because a thick layer of water is investigated; it has been customary to submerge the 5 ft. long cup system about 1 fathom below the sea surface. No considerations of magnetic disturbance arise to prohibit the use of this instrument from steel vessels other than at 'safe' depths, and there is a virtual absence of registration of spurious current from revolutions put on in response to ship movements.

Text-fig. 1 shows the instrument (the original 'Vertical Log') with which the information was gathered, and its legend tells something about the employed apparatus.

Before the War, it was customary to publish a yearly presentation of the results obtained from the various lightships aboard which the work was in

train. Such annual publication was made in the pages of the *Rapports et Procès-Verbaux* of the International Council for the Exploration of the Sea.

When War came, a considerable body of data perforce went unpublished, and to this was added information from such lightships in which it was possible to continue the work. That such continuance into the period of hostilities was sometimes possible was due jointly to the good offices of the Hydrographic Department of the Admiralty, and to the kindness of the English Department of Fisheries, in allowing the senior author not only to continue in possession of the apparatus which he had been using, but also to have the services of his assistant (the late Mr R. S. Minchin) to run the programme whilst he himself was engaged upon other duties.

Amongst the bodies of unpublished data held when the War ended was that for the Seven Stones Lightvessel. The position in question is perhaps second in interest only to that of the Varne Lightship anchored in the Straits of Dover. The amount of information is by itself noteworthy, and the position concerned has its own particular interest.

Various authors (quoted later) have put forward views on the possible scheme of water circulation in the area off the western entrance of the English Channel and the adjacent region lying off the southern entrance to the Irish Sea. It seemed that the data from the Seven Stones might serve to throw light upon this matter, or at least might provide help to anyone trying to decide whether or not the Rennell Current is a real entity.

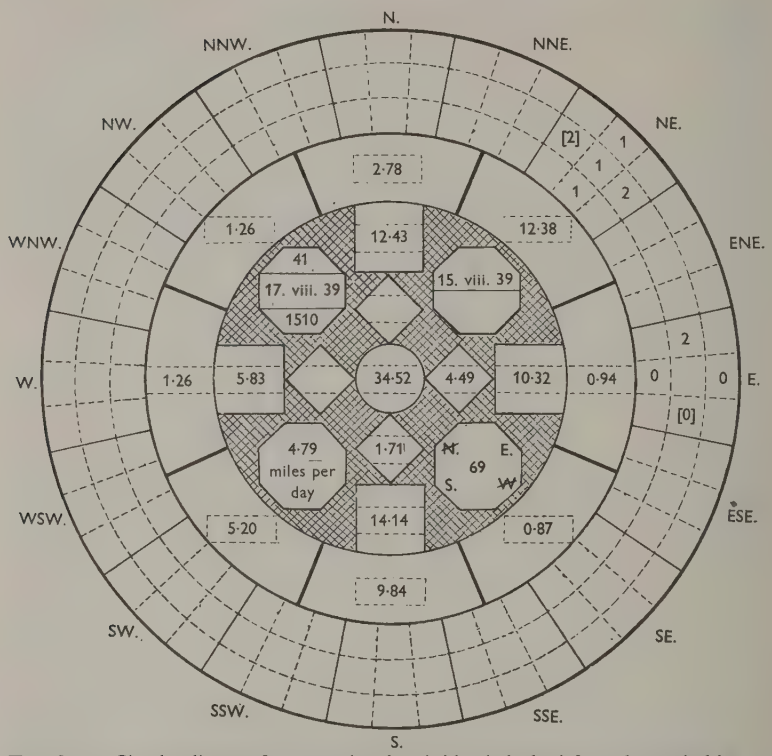
In an earlier paper (Carruthers, 1934) the Rennell Current topic was touched upon. At that time it was possible to discuss the results obtained in the course of only 28 days observing from the Seven Stones Lightship.

The instrument then used was not the same, and the depth of observation was greater, but the 1934 results testified to the existence of an overall water movement towards the south-east quadrant of the compass. This direction of residual flow, we shall see, was evidenced by the very much larger body of data to be discussed below.

It was considered that the mass of continuous data available amply merited a measure of detailed study, and it has been deemed worth while to investigate it rather thoroughly in respect of wind influence on water movement.

When the time comes to publish the collection of daily records *in extenso*, they will probably be presented in a form which lets the associated wind conditions be seen at a glance. It is intended to publish them entered in 'clockface' form, of which a specimen is included here (Text-fig. 2.)

The authors desire to express their thanks to the crew of the lightvessel, by whom the observations were made.



Text-fig. 2. Circular diagram for presenting data (with winds data) from the vertical log.

Explanation of circular diagram

OUTER RING. (Pecked squares.) The nine wind strengths (Beaufort scale) recorded for the 24 hr. upon which the observation is approximately centred.
INNER RING. The water movement in sea miles recorded against each octant during the day.
SQUARES. The gross cardinal components of the latter.
DIAMONDS. The net values of the cardinal components.
CIRCLE. The total water movement.
OCTAGONS. *Top left*—from top to bottom the *serial number*, *date* and *mid-time* of the particular observation.
Top right—the date of the nearest *new* moon in the *upper* half or of the nearest *full* moon in the *lower* half
Bottom left—the *magnitude* of the residual water movement.
Bottom right—the *direction* of the residual water movement.

THE OBSERVATIONS

Observations were commenced aboard the Seven Stones Lightvessel on 4 July 1939, when she was in a position 50° 03·3′ N., 6° 05·1′ W. After some 4 months (20 November) the vessel was moved to a position 50° 03·5′ N.,

6° 05·1′ W.; observations were, of course, interrupted during the move, but otherwise the change of position, which only amounted to 2 cables, does not seem to have disturbed the sequence of the recorded data. Work was resumed at the new position on 21 November 1939, and continued until 1 May 1941, when the vessel was withdrawn owing to the war situation.

For various reasons breaks in the observations occurred on nineteen occasions, including the one referred to above. In all, 624 observations, each lasting one lunar day, were made (although 625 observations are listed, serial numbers 132 and 133 only produced sufficient data for one observation owing to an error in the timing of the observations).

The Seven Stones Lightvessel lay in a mean depth of 40 fathoms about 2 miles to the north-eastward of the Pollard Rock, one of the Seven Stones. This position is some 14 miles due west of Land's End and 12 miles north-east of St Mary's (Scilly Isles). The passage between land and land is 22 miles wide, the mean depth being about 36 fathoms (see Text-fig. 3).

Water movements at this position were recorded on all eight octants, but the overall or residual movement was principally east-south-easterly.

During the period under review the centre of the cup system of the measuring unit was 21 ft. below the sea surface. The water-layer in which observations were taken was from 3 to 4 fathoms below the surface.

The wind was estimated every 3 hr., the strength being recorded in Beaufort scale numbers. When the local tractive effect of the wind is considered in this paper, sight is not lost of the fact that the observations relate to a water-layer well below the surface.

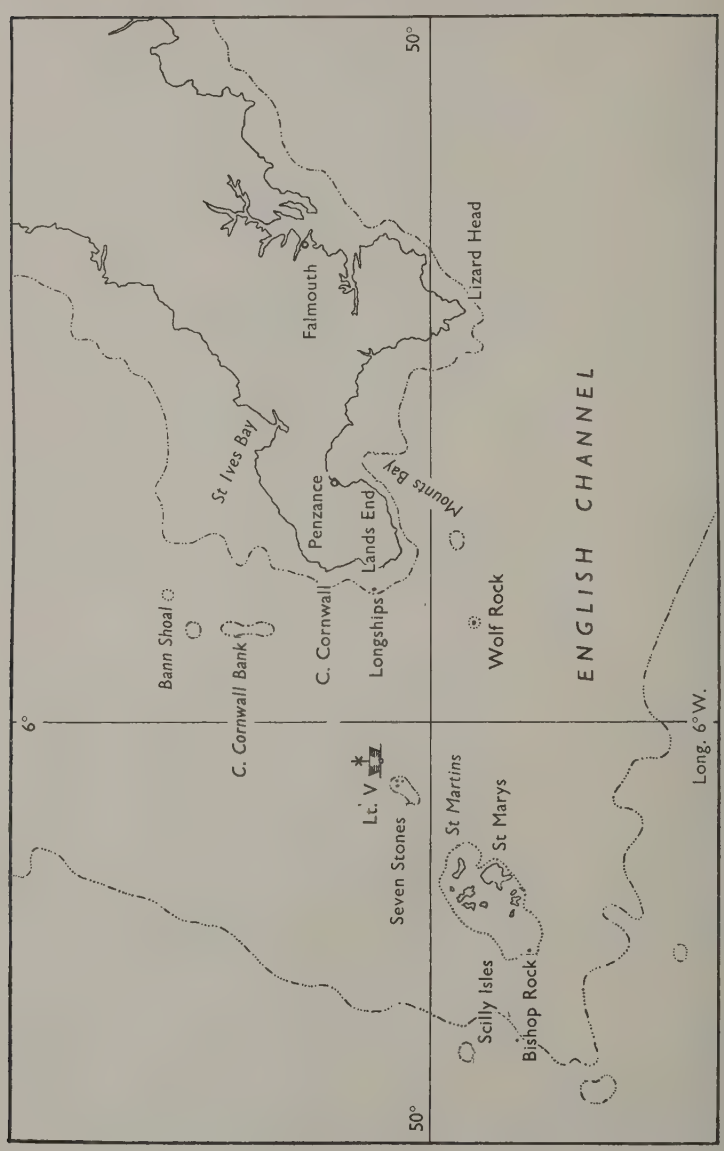
The total revolutions, and the revolutions of the eight individual octant counters, per lunar day, were simply obtained by subtracting the readings of the day before. The total daily revolutions and the sum of the revolutions on the octants agreed to within twenty-two revolutions, on the average, though very much larger discrepancies occasionally occurred. This average disagreement represents $\frac{1}{2}\%$ of the total revolutions, and was presumably due to the time lost in changing over the octant counters.

The water movement in sea miles per lunar day was obtained by applying the 'calibration constant' of the instrument to the revolutions. In this case, 300 revolutions were the equivalent of 1 mile (6080 ft.) of passing water.

The mean wind for the day was calculated by geometrically averaging the winds recorded between the initial and final readings of the counters each day.

A plot of the total water movement showed a strong resemblance to a tidal cycle, with maxima occurring from 1 to 3 days after full and new moon (see Pls. I and II). A smooth and regular curve could be drawn through a large percentage of the points.

Superficially, a plot of the magnitude of the residual water movement showed much less tendency towards regularity, but comparison with the total



Text-fig. 3. Position of Seven Stones Lightvessel.

water-movement plot revealed that it was periodic, with marked minima and with double maxima spaced on either side of the total water-movement maxima. A regular curve was also superimposed upon this plot.

(For details of the method of construction of these regular curves, see below, p. 601).

A plot was also constructed of the magnetic direction of the residual water movement, centred approximately on the mean for the whole period.

As a first step in analysis, the monthly averages of water and wind movements (shown at the tops of Pls. I and II) were investigated, as these gave reasonably smoothed values for comparison over approximately equal periods of time. It was found that the following conditions of water movement obtained in association with the mean residual wind:

(*a*) Larger *total* water movements than usual were associated with winds from east, through south, to west-north-west, while smaller movements than usual were associated with winds from other directions. 'Doubtful' sectors existed on the boundaries between the two areas. Also, lower total water movements occurred when the residual wind velocities were medium (4–8 m.p.h.), and higher when the wind velocities were both low (0–4 m.p.h.) and high (8–12 m.p.h.).

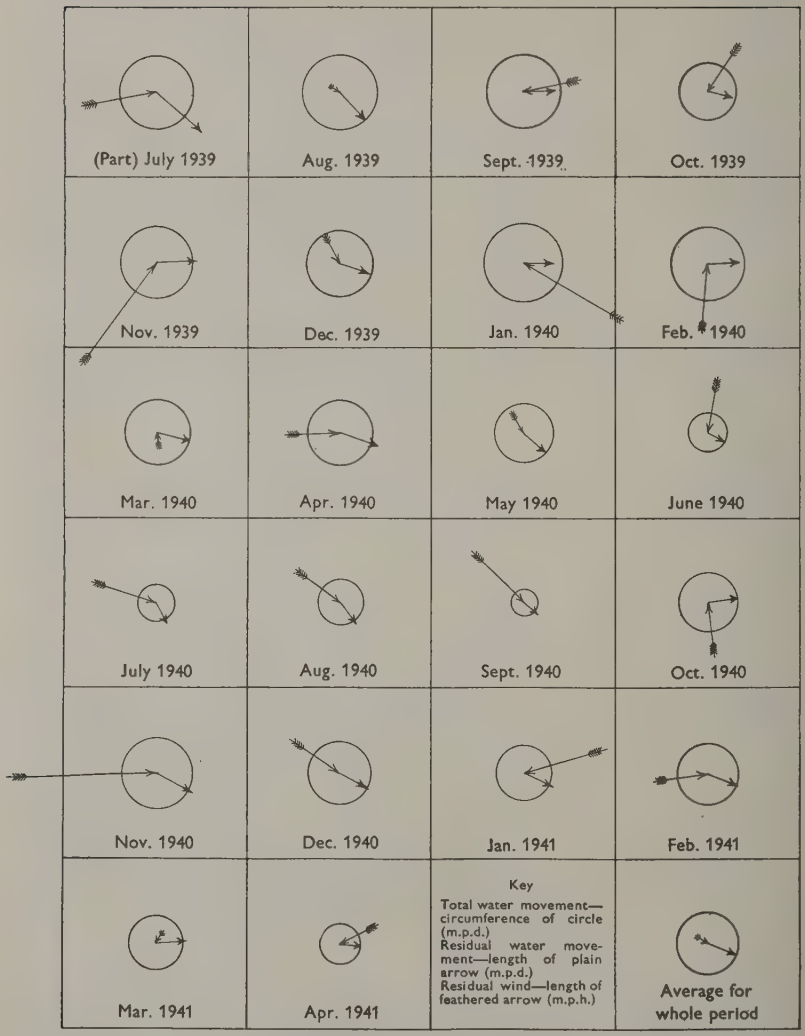
(*b*) Above average *residual* water movements were associated with winds from south-south-west to north-west, and below average movements with winds from north-west to east-south-east; when the wind was between east-south-east and south-south-west the residual water movement was of average magnitude. Also, the residual water movements tended to be lower than usual with medium winds and higher than usual with light and strong winds.

(*c*) In association with winds from north-east, through south, to south-south-west the *direction* of the residual water movement was displaced to the north of the mean for the whole period; with winds between south-west and north-north-east the direction was displaced to the south. When winds were from the small sectors between these major arcs the direction of the residual water movement remained average. Also, there seemed to be some tendency for light winds to be associated with the average direction, medium winds with a displacement to the south and strong winds with a displacement to the north of the average. Between the two last-named wind-speed groups, however, was a band where the direction was again average. There was also a single indication that a residual wind above 12 m.p.h. was associated with a displacement to the south of the average.

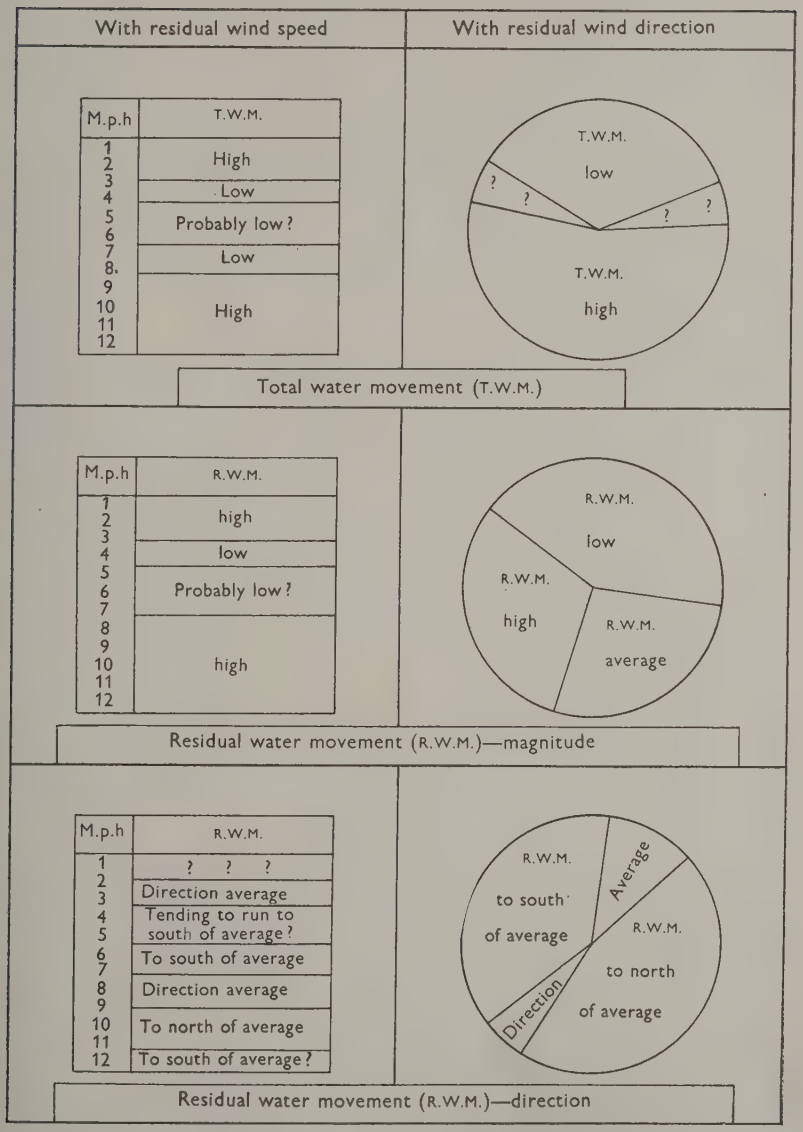
(It must be emphasized that those conclusions which are derived from wind strength are by no means as firm as those derived from wind direction.)

The monthly averages are illustrated graphically in Text-fig. 4, and the findings in Text-fig. 5.

The above findings were checked by inspection of the plotted observations of wind and water movements for individual days or groups of days, and were



Text-fig. 4. Monthly averages of total and residual water movement and residual wind. (All directions are true—variation 13½° W.)



Text-fig. 5. Association of water movements with wind. (All directions are true—variation 13½° W.)

found to agree reasonably closely, although it is not denied that there are a number of occasions when the findings appear to be in direct opposition to the facts. Obviously some unknown factor, such as the wind at some distance from the lightvessel, must have made its influence felt, and on these occasions, it is assumed, its effect was greater than that of the local wind.

The average residual water movement *over the whole period* was 2·5 m.p.h. in a direction S. $56\frac{1}{2}°$ E. (magnetic) = S. 70° E. (true). In an earlier paper (Carruthers, 1934) the senior author calculated, from twenty-eight observations made in August and September of 1933, that the residual water movement was 1·9 m.p.d. in a direction S. 20° E. (true). Obviously these earlier figures differ widely from the average of the observations here discussed; nevertheless, they agree reasonably well with the monthly averages for the August and September of 1939 and 1940.

Harvey (1924) indicated, however, that there was a northward movement of the water between Land's End and the Scilly Isles, and in a diagram showed a north-north-west movement close to Land's End forming part of a cyclonic flow round Scilly. In a later paper (1929) he stated that there was a north-north-west movement at a daily speed of $1\frac{1}{2}$ knots at a depth of 60 m., and that a cyclonic flow existed in the upper layers as a component of the currents at 60 m. Matthews (1913), who was quoted by Harvey, remarked that the northerly current passed only a few miles to the westward of Land's End. A noteworthy reference by Matthews, however, was to a paper published by Dr Bassett in which the latter stated that water from the Bristol Channel escaped into the English Channel between Scilly and Land's End.

It is of course undeniable that 13% of the observations show a residual current in the magnetic octants north-west, north and north-east, and that on a further 12% of the days it pursues courses between the limits of these octants ($67\frac{1}{2}°$ to the east and west of north) and east and west (magnetic). The monthly averages (see Text-fig. 4), however, show that during only 5 months, all winter ones, was the residual current to the north of east (true), and then by only a few degrees.

With the evidence available it would be impolitic to dispute the existence of a northerly current *close* to Land's End (some 12 miles distant) and at a greater depth. What does appear to be somewhat more doubtful is the cyclonic flow round the Scilly Isles, and in this connexion information obtained from Tizard (1909) seems to indicate the existence of an *anti-cyclonic* residual movement.

The direction of the residual current at the Seven Stones is more across than through the Land's End-Scilly passage. If the existence of an anti-cyclonic movement round Scilly can be accepted, it is suggested that the east-south-easterly residual current is perhaps an offshoot of this system which turns further to the north as it crosses the passage and finally joins the north-going flow north of the Longships. It is only fair to state, however,

that Tizard's logship observations also indicate a south-easterly residual current at three positions to the south-east of the Seven Stones. On these grounds the inference is that the residual current at the Seven Stones Lightvessel is, in fact, part of a general south-easterly flow through the passage.

Text-fig. 6 illustrates the possible circulation referred to above. The water movements are the resultants of the figures given in the tables by Tizard, assuming that the hourly observations represent the average movement for an hour.

In the study of water movements it is probably unsafe to draw analogies, but there does seem to be a certain similarity between the current systems in the North Sea and in the neighbourhood of the Scilly Isles. In the former, a north-easterly current emerges from the Straits of Dover, continues along the coasts of the Low Countries, turns more to the north off the Danish coast and finally escapes from the North Sea in a north-north-westerly direction after skirting the coast of Norway. Part of the north-westerly water movement to the west of the British Isles turns clockwise to the north of the Shetlands to enter the North Sea in a southerly direction. Some of this water turns to the eastwards to flow past the vicinity of the Fisher Banks and join the north-going movement along the Norwegian coast.

In the Scilly area, there are the east-north-easterly current up-Channel to the south of the area and the northerly current close to Land's End, while to the northward water enters the Bristol Channel from the south-west. If the analogy has force, the east-south-easterly water movement at the Seven Stones is the counterpart of the current in the Fisher Banks area. Until data are available of water movements in other positions in the vicinity, however, suggestions such as these must perforce be in the nature of speculation.

Turning to the plotted information, there are notably small minimal total water movements (less than 1 mile per day) between the end of July and the end of September 1940. Minimal total water movements of less than 4 miles a day also occur in October 1939, and January, March and April 1941. These minima are not associated with any particular wind direction nor, with the exception of the one occurring in January 1941, with particularly strong winds.

This was considered sufficiently striking to warrant calling upon the local knowledge of the lightvessel personnel, and a letter of inquiry was accordingly addressed to the competent Trinity House authority.

In his reply to the Chief Superintendent of Trinity House, one of the masters of the lightvessel (Mr D. Appleby) remarks that on some days a 2 lb. lead can be kept on the bottom during the whole of the tidal cycle, flood and ebb. Bearing in mind how very little water movement is necessary, in 40 fathoms, to take such a light weight off the bottom, it can safely be assumed that the tidal stasis on such occasions extends from the surface to the sea-bed. Mr Appleby adds that these periods occur during neap tides, especially when the succeeding spring tides are not 'very hot', providing weather conditions

Text-fig. 6. Possible circulation in Scilly-Land's End area.

are normal. A glance at the plotted observations for the dates referred to will show that Mr Appleby's statements are in good agreement.

Scrutiny of the plotted record of total water movement will also reveal that, if a smoothed curve were drawn through it, the resultant curve would exhibit sinusoidal characteristics. It is suggested that the minimal total water movements coincide with the minima of such a smoothed curve, which occasionally approaches very close to the zero line, and that they are therefore regular and would be predictable occurrences. Indeed Mr Appleby predicts in his letter, which was written in 1947, that minimal movements would occur on about 24 or 25 September of that year; unfortunately there are no records to confirm this. It appears possible that the period of these minima is about twice yearly, and that they have alternate higher and lower values.

A further point of interest arises in connexion with the plotted observations of residual current direction. Nearly always the direction changes, usually in a marked manner, from one side of the mean to the other at, or shortly after, the minima of the total water movement (i.e. neaps). This shift is mostly from south to north of the mean direction. At about the time of springs there is a shift to the south of the mean, but this movement is very much less marked and may take some days to accomplish. The shifts may sometimes be of degree and not of 'sign'. Viewed in this light, the otherwise irregular plot of residual current direction exhibits 'saw-tooth' characteristics with reasonably well-marked periodicity.

Again, if a smoothed curve were drawn through the residual current-direction plot, the resultant curve would oscillate from side to side of the mean direction. From Pl. I, which covers 1 year, it is tempting to assume that the oscillation is annual, with maximum northerly deflexion in winter and maximum southerly in summer, but Pl. II, for the succeeding 10 months, does not confirm this, and the point must await the collection of more data.

Summarized Results

A survey of the water and wind movements recorded during the 624 days of observing at the Seven Stones Lightvessel brings the following facts of chief interest to light:

(i) Water moved towards all octants of the compass.

(ii) The maximum/average/minimum values of the total water movement (the summed daily mileage of the travel in all eight octants) were 39·7/15·0/0·2 miles/day.

(iii) The daily water movements in the individual octants are given in miles per day in Table I.

Table I.

Octant (magnetic)	N.	N.E.	E.	S.E.	S.	S.W.	W.	N.W.
Maximum	5·1	13·7	5·8	5·4	14·7	7·3	5·5	3·7
Average	1·3	3·8	1·2	1·2	4·0	1·5	1·0	0·9
Minimum	0·0	0·0	0·0	0·0	0·1	0·0	0·0	0·0

(iv) The maximum/average/minimum residual current (the net travel or 'overall make' of the water) and its direction of flow (magnetic) were:

11·0 m.p.d. towards S. 15° W.,
2·5 m.p.d. towards S. 56½° E. (vector resultant),
0·1 m.p.d. towards N. 47° E.

(v) The residual water movements in the individual octants are given in miles per day in Table II, together with the percentage frequency with which they occurred.

TABLE II

Octant (magnetic)	N.	N.E.	E.	S.E.	S.	S.W.	W.	N.W.
Maximum	4·6	10·1	10·0	8·7	11·0	5·8	4·0	1·2
Average	2·7	3·6	3·6	3·4	3·7	1·7	2·0	0·8
Minimum	1·4	0·1	0·3	0·1	0·6	0·1	0·4	0·4
Frequency %	1·0	11·4	27·4	29·6	26·3	3·2	0·5	0·6

(vi) The maximum/average/minimum residual wind, expressed as a vector resultant for a whole day, and its direction, were:

38·5 m.p.h. from north-west by north (magnetic),
1·1 m.p.h. from west-north-west (magnetic).
Nil

(vii) The residual winds on the individual octants, expressed as a mean for a whole day, are given in miles per hour in Table III, together with the percentage frequency with which they occurred.

TABLE III

Octant (magnetic)	N.	N.E.	E.	S.E.	S.	S.W.	W.	N.W.
Maximum	31·3	29·6	35·8	31·3	36·2	33·6	30·8	38·5
Average	9·0	13·3	13·3	12·8	13·1	11·9	12·4	11·1
Frequency %	11·1	10·1	13·9	8·8	8·0	14·6	14·9	18·1

In addition, there was no wind on 1 day, and on 2 days the vector resultant of the winds was nil (0·5% frequency).

Correlation between Wind and Water Movement

In order to study graphically the effect of an outside influence (the wind) on daily water movement it is first essential to construct some form of ideal curve. The latter is defined as that curve which will pass through all the readings of water movement/time (graphically plotted) should external factors be neglected and only the effect of spring and neap tides be considered. A number of such ideal curves were constructed during the analysis of the Seven Stones data. The final object was to produce an ideal residual water-movement curve which would enable large deviations of the actual readings from this curve to be studied in conjunction with a graphical representation of wind strength and direction. Results in one form or another would then be obtainable, but the

accuracy of the deductions drawn from these results would naturally be dependent upon the accuracy of the ideal curve.

The residual water movement in general showed a definite tendency towards periodicity, and therefore Fourier analysis would show it to be composed of an infinite number of harmonics of a fundamental curve. Very few of these harmonics can be introduced into an ideal curve because of the difficulty of their construction, and indeed most of the harmonics are spurious, being explicable in terms of wind and other effects.

From the water-movement data the following components were obtainable:

(i) Total water movement for the whole day over the octantal headings.

(ii) Residual water movement in strength and direction.

(iii) $N+S$ and $E+W$ components of the total water movement.

(iv) $N \sim S$ and $E \sim W$ components of the residual water movement.

(*Note*. All the above water movements were measured in sea miles per lunar day.)

The $N+S$ and $E+W$ components of the total water movement were first plotted (see Pls. III and IV) and the two resultant shapes studied (plots K and L). It was found that the springs and neaps were readily discernible and that their total periods were equal to 28 ± 1 lunar days. In accordance with tidal analysis it was assumed that the two ideal wave forms required were each composed of two waves, one of period 28 days and the other of half-yearly period. On this assumption two smooth curves were drawn for the $N+S$ and $E+W$ components (curves K and L) and were found to pass through approximately one-third of the points.

Since the readings of the vertical log current meter were taken on the octantal headings the following relationships hold:

($N+S$ component) of the total water movement $= N+S+0{\cdot}7\ (NE+SE+NW+SW)$ readings.

($E+W$ component) of the total water movement $= E+W+0{\cdot}7\ (NE+SE+NW+SW)$ readings.

Therefore: ($N+S$ component) together with ($E+W$ component),

$$= N+S+E+W+1{\cdot}4\ (NE+SE+NW+SW)$$

$$= \text{total water movement (plot E)} + 0{\cdot}4\ (NE+SE+NW+SW).$$

With the negative correction term $0{\cdot}4\ (NE+SE+NW+SW)$ applied, the ideal curve for the total water movement (curve E) was obtained from the $N+S$ and $E+W$ component curves. This curve was later studied in conjunction with the wind.

In the same manner the readings for the $N \sim S$ and $E \sim W$ components of the residual water movement (R.W.M.) were plotted for magnitude *and direction*. On studying the two shapes obtained (plots M and N) it was found that the movements were periodic as before. However, in most cases where there was a maximum in the $(N+S)$ or $(E+W)$ curves there was a minimum in the

$N \sim S$ and $E \sim W$ plots. It was therefore deduced that a maximum component of total movement did not mean a maximum component of residual movement, but rather a maximum change in magnitude (a change in direction being regarded as a further change in magnitude). Thus for every maximum in a total component curve there would be two maxima and one minimum in the corresponding residual component curve. Assuming this, and that the waves comprising the ideal curves were again of periods 28 days and half yearly, curves M and N were drawn for the $N \sim S$ and $E \sim W$ residual components. The wind appeared to have a greater effect on the component water movements and the ideal curves passed through only one quarter of the points.

Resolving vectorially, the resultant residual water movement is equal in magnitude to

$$\sqrt{[(N \sim S \text{ comp.})^2 + (E \sim W \text{ comp.})^2]},$$

and therefore its ideal curve (curve G) could then be constructed from the two component curves. The actual residual readings were then plotted with respect to magnitude only (plot G) and the ideal curve was found to be in fair agreement.

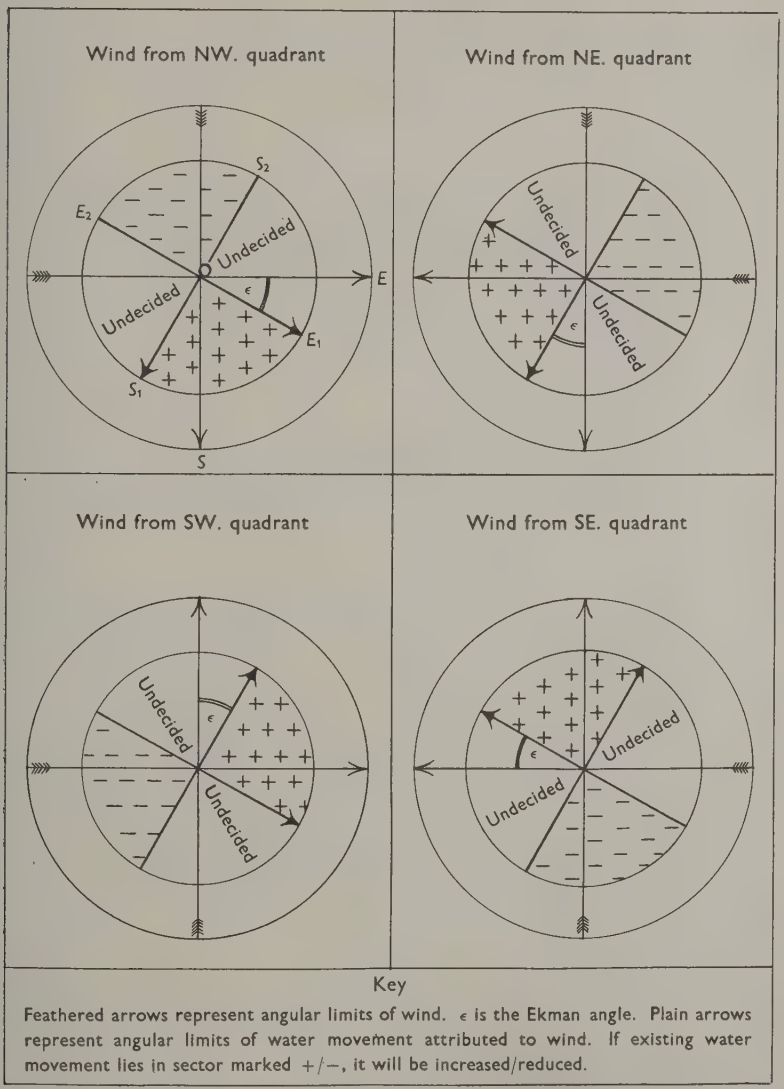
Finally, the wind was analysed into $N \sim S$ and $E \sim W$ components and its force reverted to Beaufort scale. The two components were plotted in magnitude and direction and the plots (H) studied in relation to large deviations from the ideal curves. The following deductions were made assuming that the non-factual curves were authentic.

On comparing the ideal residual water movement (R.W.M.) curve (G) with the observed plot, it was found that although on the whole there was a definite agreement between the two, for a number of observations there was a marked divergence in magnitude. Considering the ideal curve as a datum, a positive divergence was said to exist if the factual plot was above the curve and a negative divergence if below. Noting the wind components where the divergences occurred, a table of the following form was prepared:

No. of observation	Residual water movement		Wind (Beaufort scale)			
	Direction	+ve or −ve divergence	N.	S.	E.	W.
27	S. 20° E.	+6·5 m.p.d.	2	—	—	3

The table was studied with the object of relating the divergences to wind effect. Considering in each case the wind and the direction of the R.W.M. as belonging to one of the quadrants, the frequency of positive and negative divergences was found for each of the quadrants. From this frequency distribution it was discovered that the effect of the wind on the R.W.M. followed a logical hypothesis.

Text-fig. 7 is a diagrammatic representation of wind effect for each quadrant. Considering the north-west quadrant alone, the limits of the wind


Wind from NW. quadrant
Wind from NE. quadrant
Wind from SW. quadrant
Wind from SE. quadrant
Undecided
E
S
E1
E2
S1
S2
ϵ
Key
Feathered arrows represent angular limits of wind. ϵ is the Ekman angle. Plain arrows represent angular limits of water movement attributed to wind. If existing water movement lies in sector marked +/−, it will be increased/reduced.

Text-fig. 7. Theoretical effect on residual water movement of winds from various quadrants.

direction lie along OE, OS. Ekman's theory states that for the northern hemisphere, due to the effect of the earth's rotation, the direction of a water movement produced by a wind is to the right of the wind direction. Assuming that the angle between the two directions is of magnitude ϵ, the limits of the direction of the water movement produced by the wind lie along OE_1, OS_1.

Considering the limiting cases, a water movement in direction OE_1 will assist any R.W.M. whose direction lies in the semicircle S_1, E_1, S_2, thereby causing a positive divergence. It will oppose any R.W.M. whose direction lies in the semicircle S_1, E_2, S_2, and will create a negative divergence. Likewise a water movement in direction OS_1 will assist any residual water movement whose direction lies within the semicircle E_1, S_1, E_2, and will oppose a residual water movement whose direction lies within the semicircle E_1, S_2, E_2.

For a combination of the limiting cases, i.e. the effect of a general wind from the north-west quadrant, there will be a definite positive divergence for the quadrant bounded by OE_1, OS_1, and a definite negative divergence for the quadrant bounded by OE_2, OS_2; the other two quadrants will be undecided, for, although the strengths of the N and W components are known, it cannot be ascertained whether the effects of the components are directly proportional to their strengths, i.e. a N wind of force 2 might have a greater effect than a W wind of force 3 (see Text-fig. 5).

These arguments were applied to all four of the wind quadrants and the diagrams produced as shown. Of 180 cases considered, where a definite positive or negative divergence should have occurred, 80% were found to be in agreement with the above hypothesis. It should be noted that the latter is of a very general nature, and it is again emphasized that its validity depends entirely on the authenticity of the ideal residual water-movement curve.

Text-fig. 8 represents an attempt to explain vectorially the effect of a constant wind on the residual water movement. The only assumption required is that in the northern hemisphere the direction of a water movement produced by a wind is to the right of the wind direction (Ekman's theory). The results from the vector analysis can be used with the ideal R.W.M. curve shown in Pl. III. The following demonstrates that a deduction can then be made regarding the magnitude of the angle between the directions of the wind and the water.

Wind direction (from) = N. ϕ E.

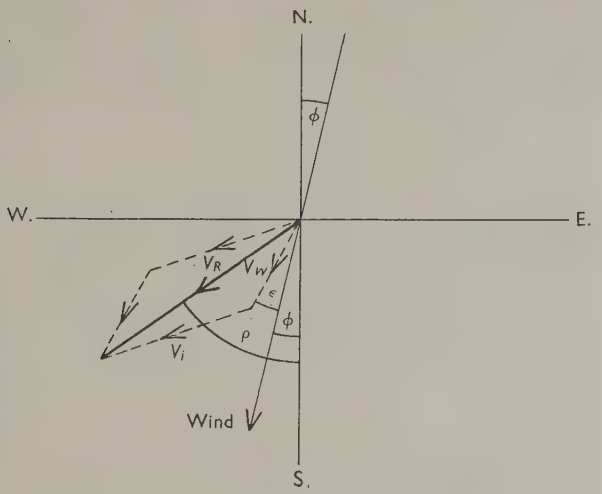
Angle between wind and water movement produced by wind (Ekman angle) = ϵ.

Direction of R.W.M. = S. ρ W.

V_R = velocity of R.W.M.

V_i = velocity of intrinsic water movement, i.e. the water movement if wind had not been present (given by the ideal R.W.M. curve).

V_w = velocity of water movement due to wind.



Text-fig. 8. Effect of wind on intrinsic water movement.

Then
$$V_R = V_i + V_w. \tag{A}$$

In the triangle of sides V_R, V_i, V_w, the angle between V_R and $V_w = \rho - (\phi + \epsilon)$.

Then
$$V_i^2 = V_R^2 + V_w^2 - 2V_R.V_w.\cos(\rho - (\phi + \epsilon)). \tag{B}$$

But from Thorade (1914)

$$V_w = \frac{1{\cdot}26V}{\sqrt{(\sin\lambda)}} \text{ for winds above Beaufort strength 3,} \tag{C}$$

where V = wind velocity and λ = latitude.

Since V_R, ϕ and ρ are known and V_i is obtainable, ϵ may be determined.

In (C), V_w is in cm./sec. and V in m./sec. Converting to other units and substituting 50° for λ:

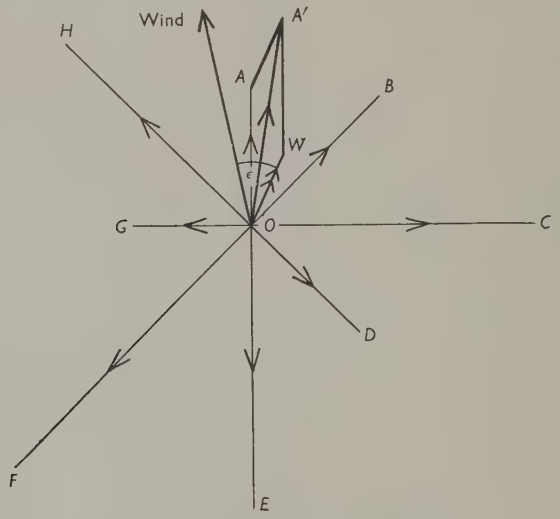
$$V_w \text{ (m.p.d.)} = 0{\cdot}35\ V \text{ (m.p.h.)}, \tag{D}$$

or, water movement = $1\frac{1}{2}\%$ of wind movement.

Rearranging (B):
$$\epsilon = \rho - \phi - \cos^{-1}\frac{(V_R^2 + V_w^2 - V_i^2)}{2V_R.V_w}. \tag{E}$$

For a number of observations, the mean ϵ was found to be 12° to the right of the wind. This is in accordance with Ekman's theory and supports, to some degree, the validity of the ideal R.W.M. curve.

It may be argued that the daily R.W.M. does not exist as a single vector, but is the resultant of several vectors each of which are acted upon by the wind. This is, of course, a fact, but reference to Text-fig. 9 will show that the foregoing analysis is not materially affected.



Text-fig. 9. Effect of wind on residual water movement components.

Consider a number of water movements acting at a point *O*. If the R.W.M. be **OR**, then

$$\mathbf{OR} = \mathbf{OA} + \mathbf{OB} + \mathbf{OC} + \ldots + \mathbf{OH}.$$

Now consider another water movement, **OW**, produced by the wind, acting in conjunction with each. Then

$$\begin{aligned}
\mathbf{OA} + \mathbf{OW} &= \mathbf{OA}' \\
\mathbf{OB} + \mathbf{OW} &= \mathbf{OB}' \\
&\cdots \\
\mathbf{OH} + \mathbf{OW} &= \mathbf{OH}'
\end{aligned}$$

If the new R.W.M. be represented by **OR**′, then

$$\begin{aligned}
\mathbf{OR}' &= \mathbf{OA}' + \mathbf{OB}' + \ldots + \mathbf{OH}' \\
&= (\mathbf{OA} + \mathbf{OW}) + (\mathbf{OB} + \mathbf{OW}) + \ldots + (\mathbf{OH} + \mathbf{OW}) \\
&= \mathbf{OR} + n.\mathbf{OW}.
\end{aligned}$$

Thus the new R.W.M. is equivalent to the old resultant acted upon by a vector of magnitude n.**OW**.

However, since **OA**, **OB**, etc. do not act for the whole time, but only for times (say) t_a, t_b, etc.

$$n = \frac{t_a + t_b + \text{etc.}}{\text{Total time}} = 1.$$

Therefore, $\mathbf{OR}' = \mathbf{OR} + \mathbf{OW}$.

Directly related to the matter of considering the wind as producing a water movement within an area of sea already possessing its own intrinsic movement is the finding of Carruthers (1941). In the experiments cited, the area concerned was one having tidal streams of continually varying magnitude and direction. It was established beyond any doubt that the winds affected the water movements to a marked degree, not only on the surface but to a depth of several feet. The effect was such that, given a persistent wind from any quarter, the tidal streams were found to produce an overall movement roughly downwind.

Summary

A review is given of the results obtained from upwards of 600 days of current measuring at the Seven Stones lightvessel during 1939–41. From the plotted observations, an attempt is made to deduce the association between the total daily water movement, irrespective of direction, the residual daily water movement or current, and the mean local residual wind.

The average residual water movement over the whole period was 2½ m.p.d. towards east-south-east. Statements made by earlier authors regarding the water circulation in adjacent areas are examined, and reconciliations are suggested where they seem to conflict with this finding.

An endeavour is made to correlate the wind and water movement mathematically.

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EXPLANATION OF PLATES

Plate I

Water movement and wind at the Seven Stones Lightvessel, July 1939 to July 1940.

Plate II

Water movement and wind at the Seven Stones Lightvessel, July 1940 to April 1941.

Key to Plates I and II

A: Average total daily water movement during the month, in miles per day.
B: Average residual daily water movement and direction (vector resultant) during the month, in miles per day.
C: Average of mean residual daily wind and direction (vector resultant) during the month, in miles per hour.
D: Full and new moon.
E: Total daily water movement, in miles per day, i.e. the sum of the water movements in all octants, regardless of direction. The thick line represents the recorded observations; the thin line is the 'ideal' curve.
F: Direction of residual daily water movement, i.e. the vector resultant in all octants.
G: Residual daily water movement, in miles per day, i.e. the resultant of the water movements in all octants. The thick line represents the movement calculated from the recorded observations; the thin line is the 'ideal' curve.
H: Mean daily residual wind force and direction, in Beaufort scale. The full line represents northerly and southerly winds; the pecked line easterly and westerly winds.
J: Calendar; the alternate black and white bars represent weeks of seven solar days.

Notes. (i) All miles are '*sea* miles' of 6080 ft. (ii) All days are *lunar* days of 24 hr. 50 min., unless otherwise stated. (iii) All directions are *magnetic.*

Plate III

Components of water movements at the Seven Stones Lightvessel, July 1939 to July 1940.

Plate IV

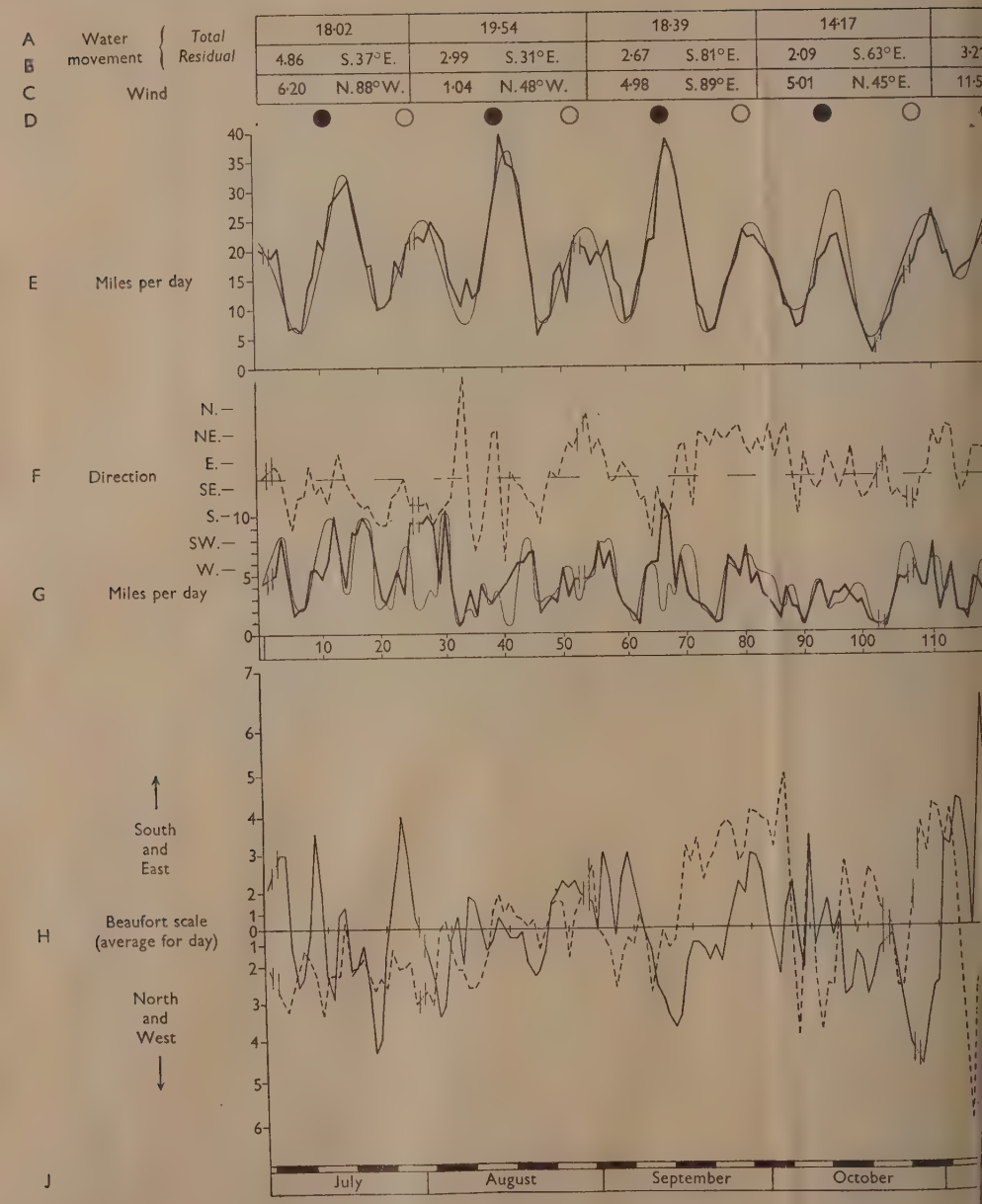
Components of water movements at the Seven Stones Lightvessel, July 1940 to April 1941.

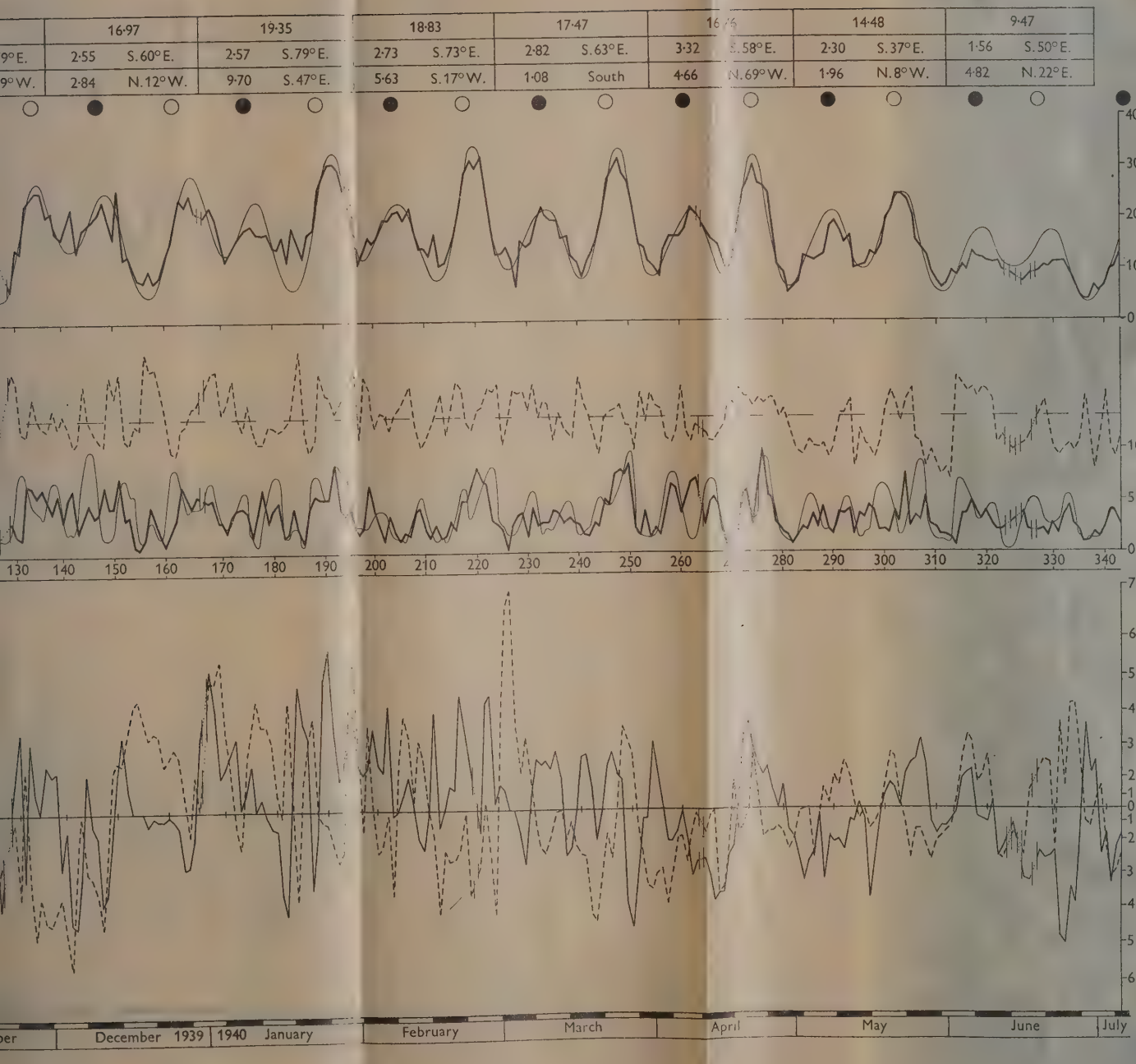
Key to Plates III and IV

K: North+south component of total daily water movement, in miles per day.
L: East+west component of total daily water movement, in miles per day.
M: North-south component of residual daily water movement, in miles per day.
N: East-west component of residual daily water movement, in miles per day.

Notes. (i) All miles are '*sea* miles' of 6080 ft. (ii) All days are *lunar* days of 24 hr. 50 min. (iii) All directions are *magnetic.* (iv) The thick lines represent the movements calculated from the recorded observations; the thin lines are the 'ideal' curves.

			18·02		19·54		18·39		14·17		
A	Water movement	*Total*	4.86	S.37°E.	2·99	S.31°E.	2·67	S.81°E.	2·09	S.63°E.	3·2
B		*Residual*									
C	Wind		6·20	N.88°W.	1·04	N.48°W.	4·98	S.89°E.	5·01	N.45°E.	11·5




16·97
19·35
18·83
17·47
14·48
9·47
9° E.
2·55 S. 60° E.
2·57 S. 79° E.
2·73 S. 73° E.
2·82 S. 63° E.
3·32
2·30 S. 37° E.
1·56 S. 50° E.
9° W.
2·84 N. 12° W.
9·70 S. 47° E.
5·63 S. 17° W.
1·08 South
4·66
1·96 N. 8° W.
4·82 N. 22° E.
A
B
C
D
E
F
G
H
J
N.
E.
S.
W.
130 140 150 160 170 180 190 200 210 220 230 240 250 260 280 290 300 310 320 330 340
December 1939
1940 January
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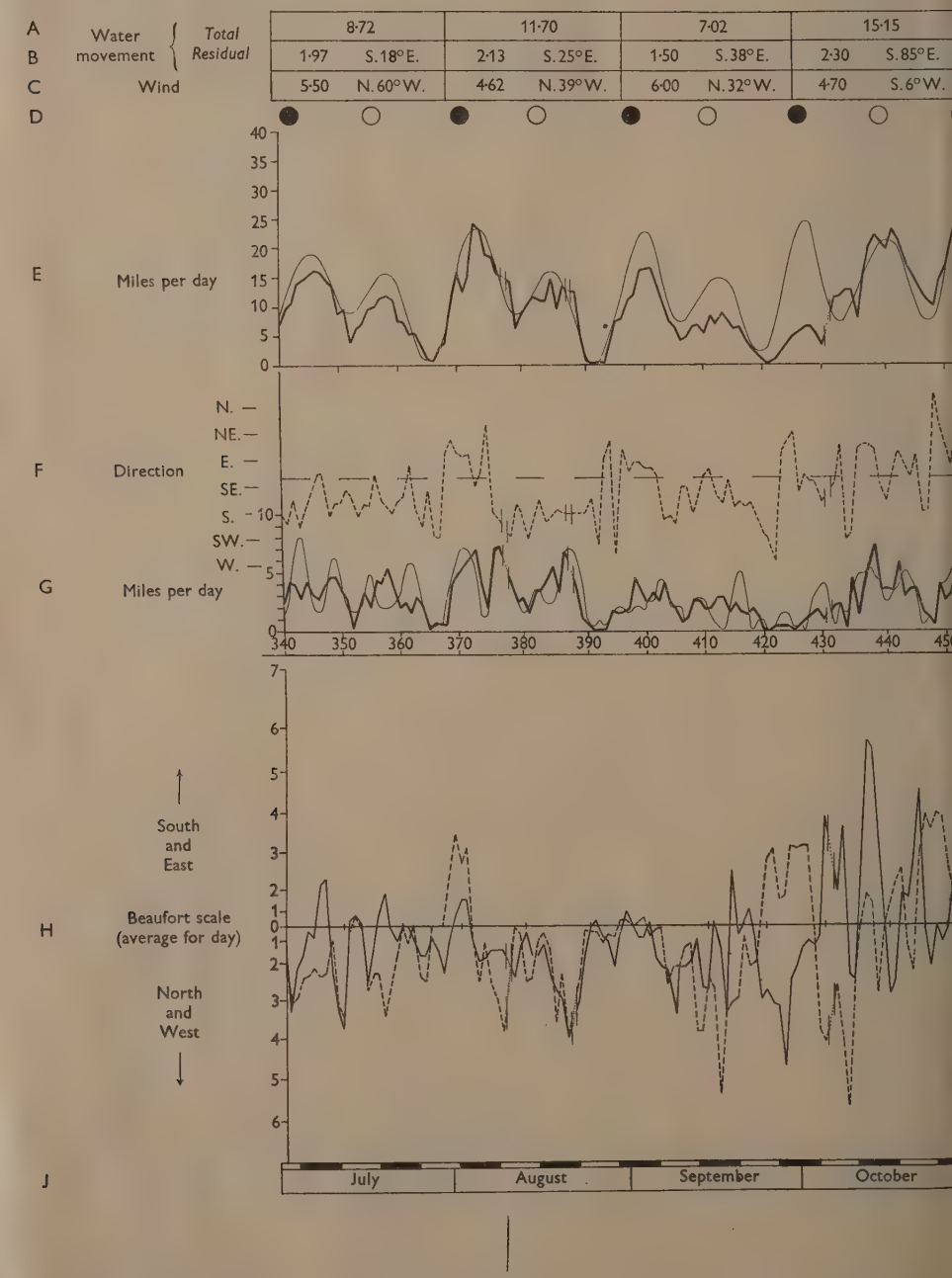
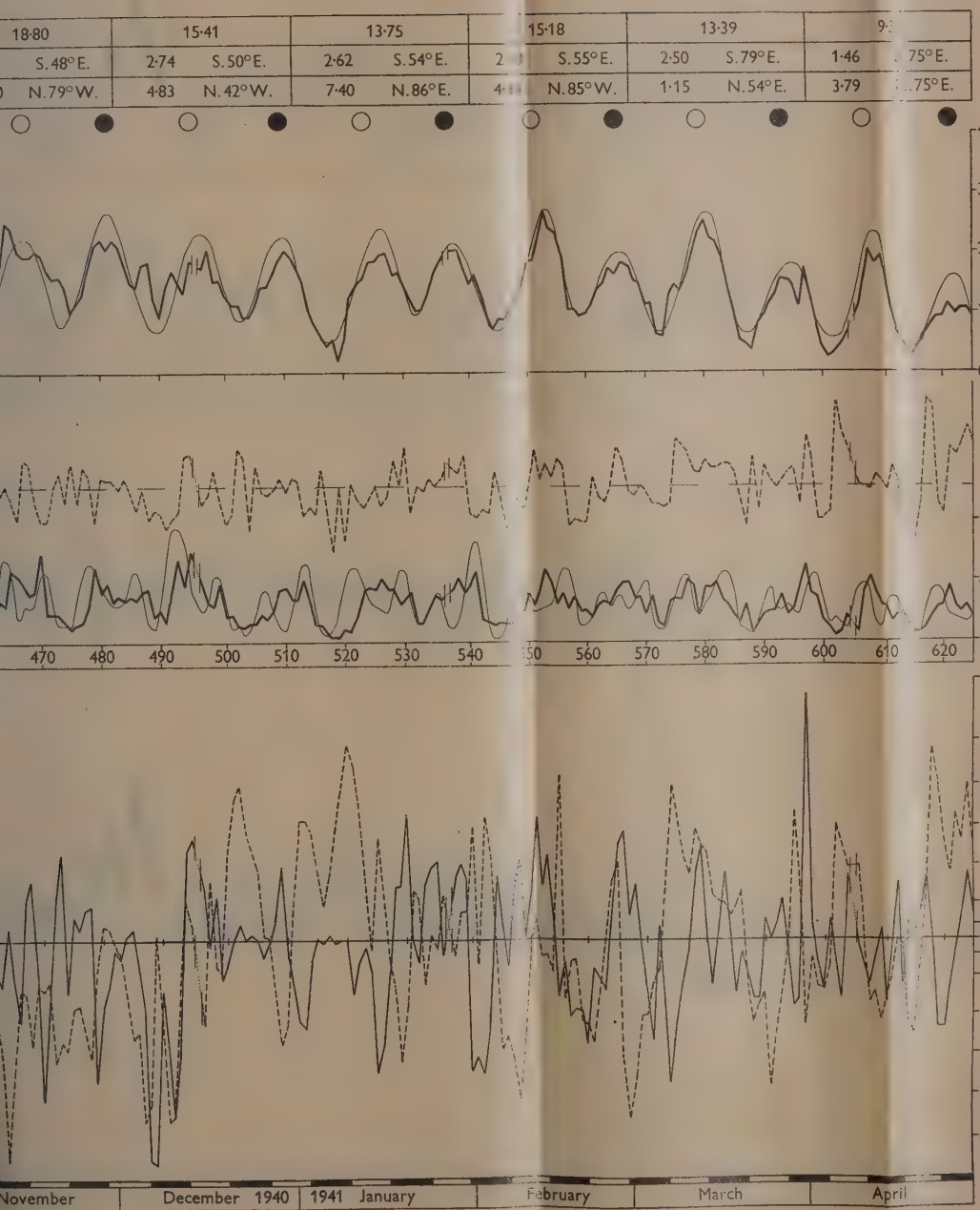
March
April
May
June
July


A
B
C
D
E
F
G
H
J
Water movement
Total
Residual
Wind
8·72
11·70
7·02
15·15
1·97
S.18°E.
2·13
S.25°E.
1·50
S.38°E.
2·30
S.85°E.
5·50
N.60°W.
4·62
N.39°W.
6·00
N.32°W.
4·70
S.6°W.
Miles per day
Direction
N.
NE.
E.
SE.
S.
SW.
W.
Miles per day
South and East
Beaufort scale (average for day)
North and West
July
August
September
October


18·80
15·41
13·75
15·18
13·39
S. 48° E.
2·74
S. 50° E.
2·62
S. 54° E.
S. 55° E.
2·50
S. 79° E.
1·46
N. 79° W.
4·83
N. 42° W.
7·40
N. 86° E.
N. 85° W.
1·15
N. 54° E.
3·79
A
B
C
D
E
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G
H
J
40
30
20
10
0
N.
E.
S.
W.
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November
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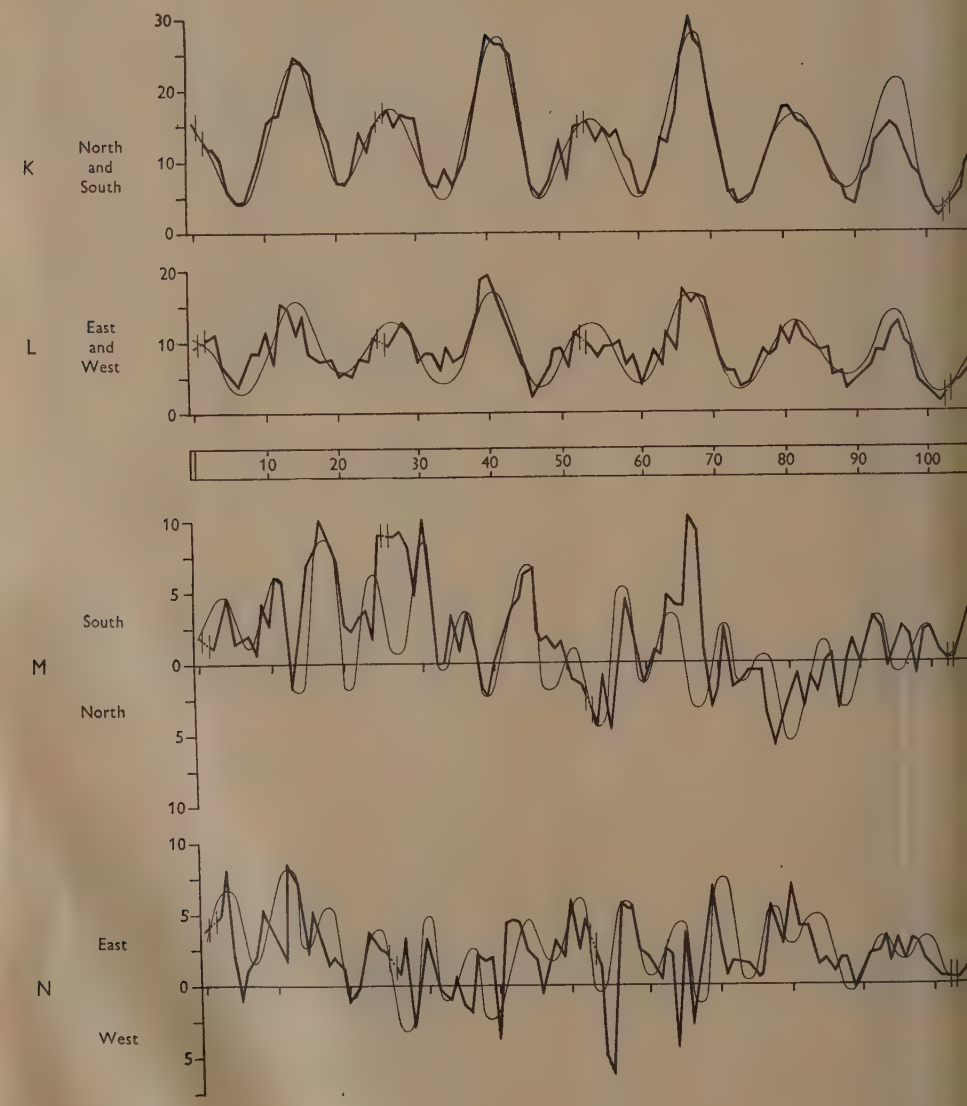
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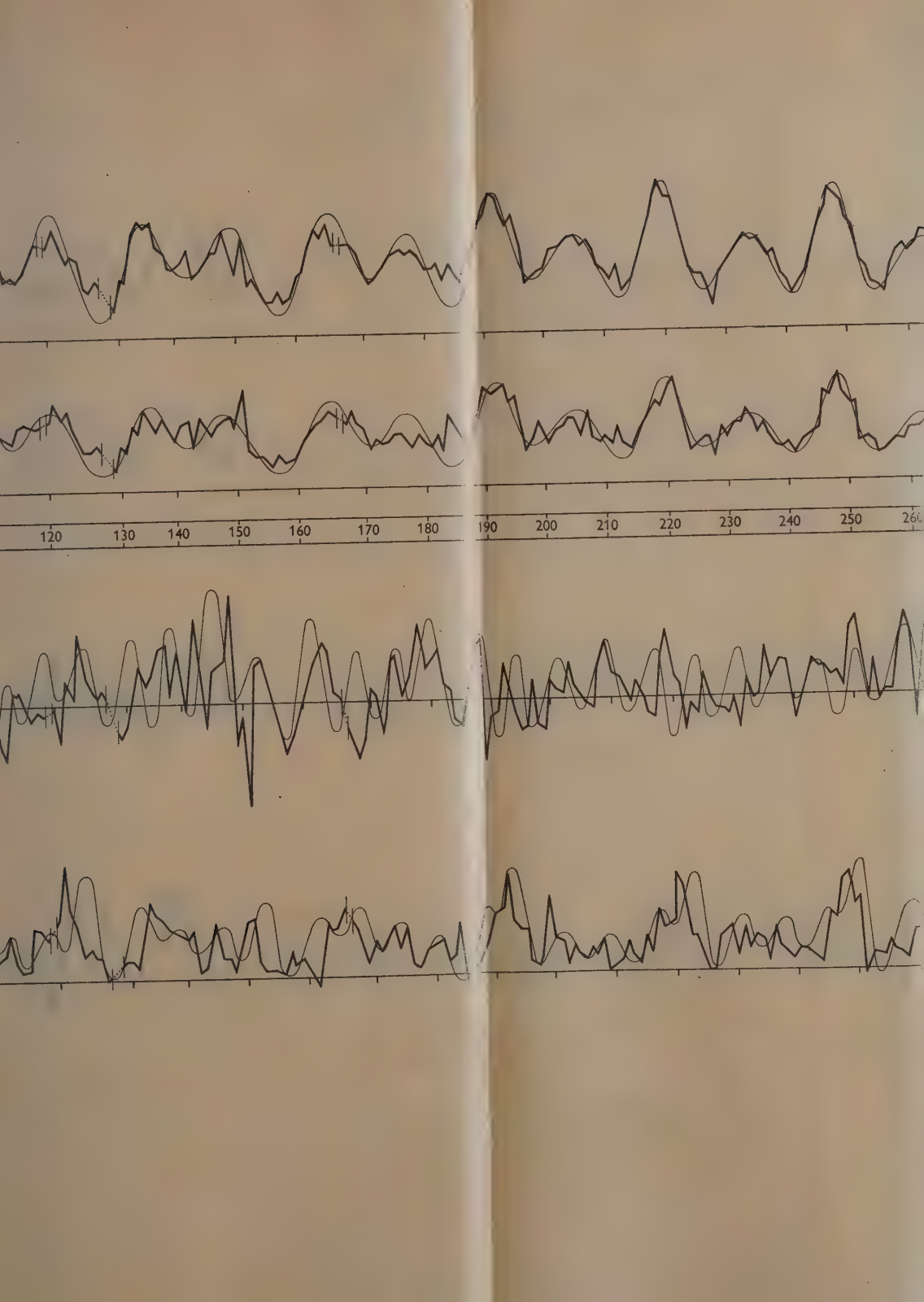
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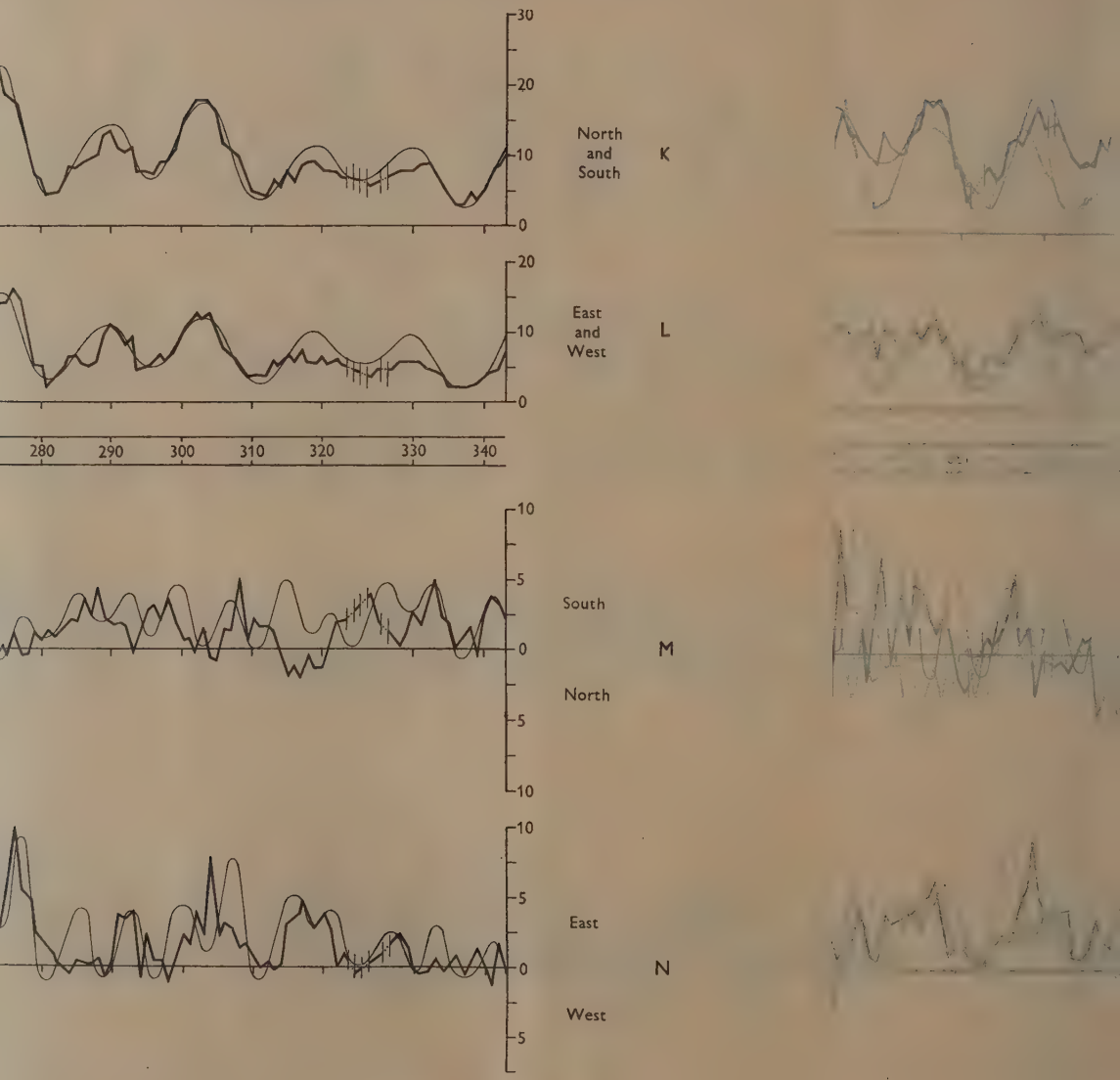
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West
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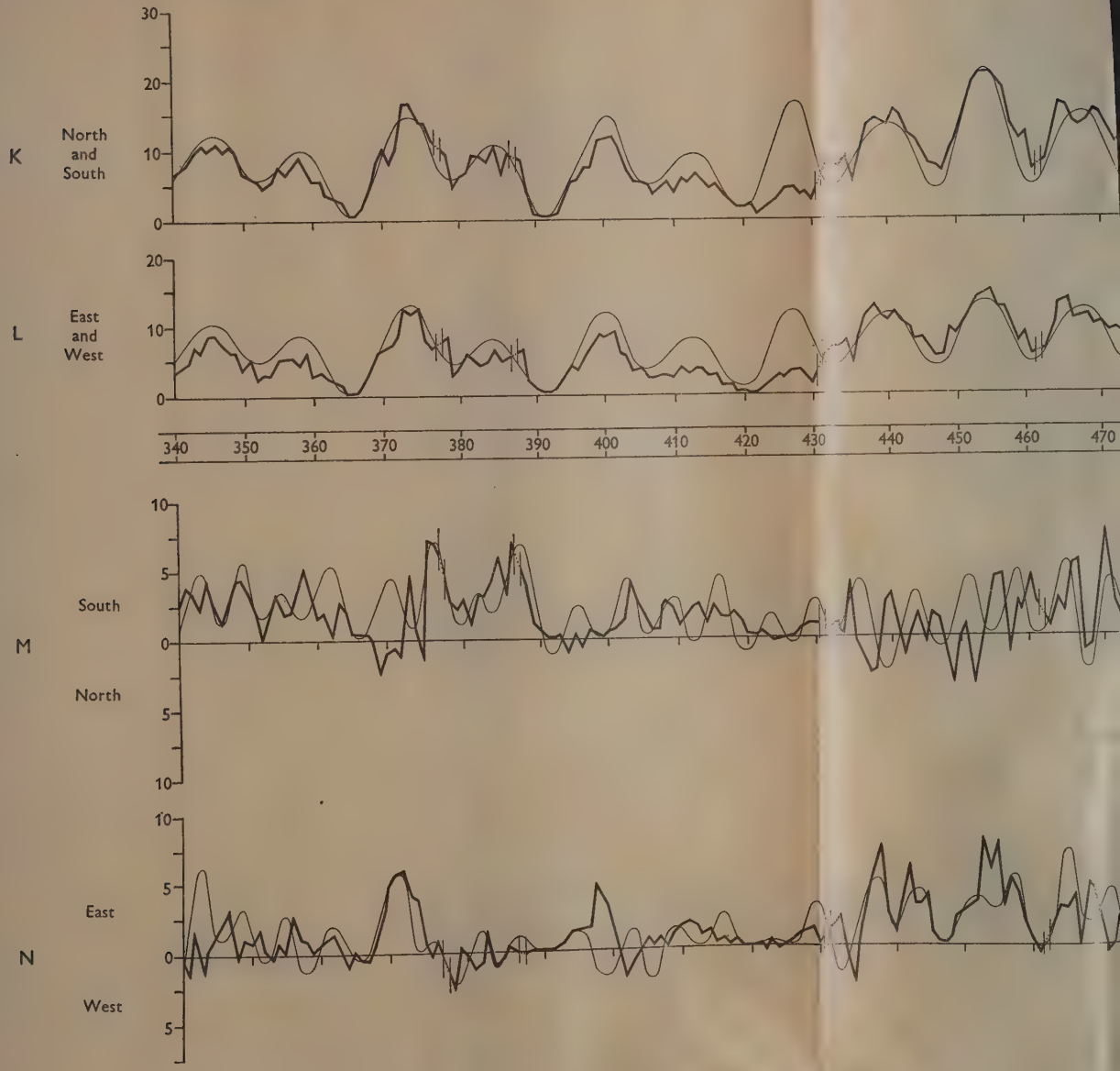
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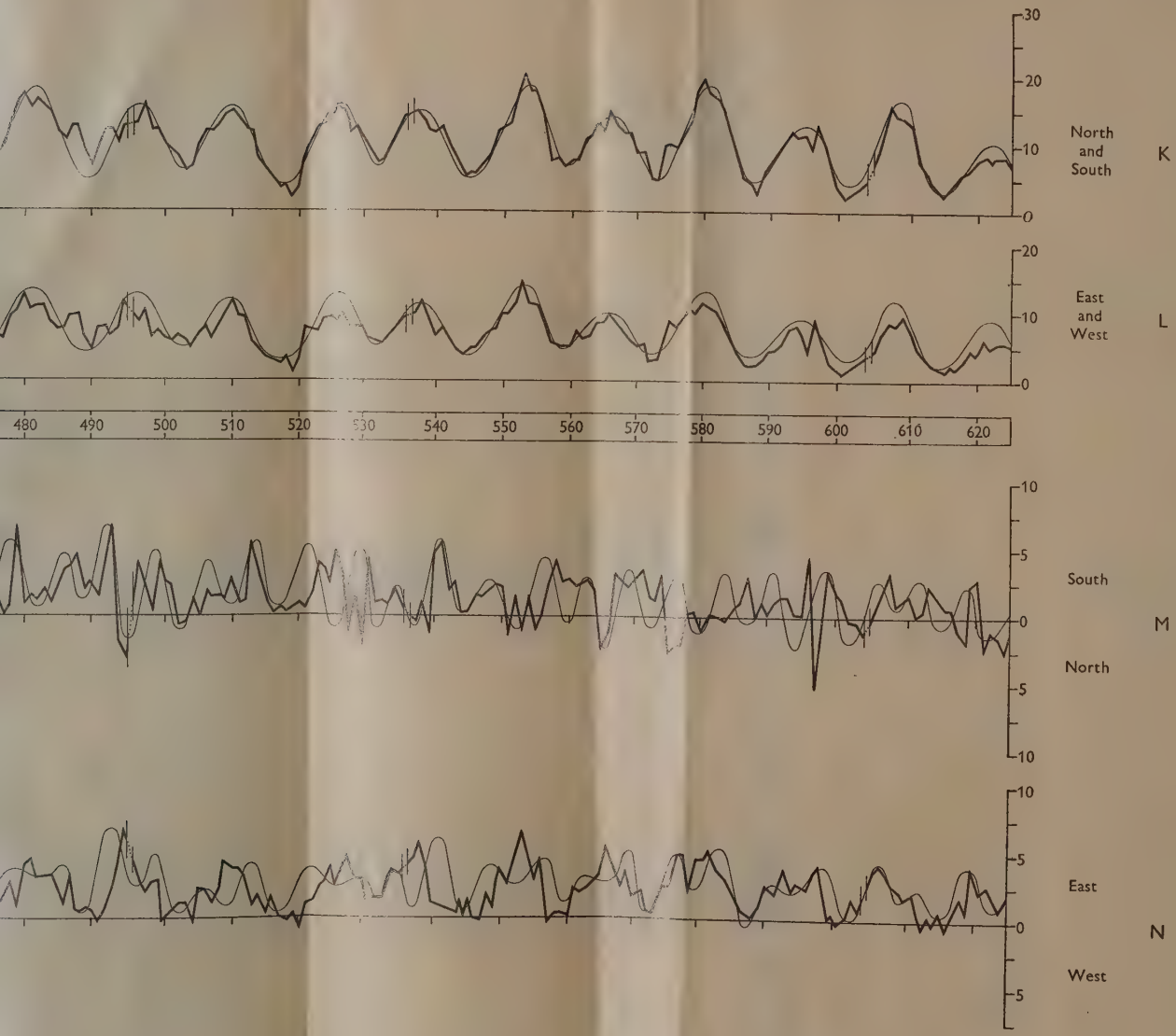
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SEASONAL CHANGES IN THE PHYTOPLANKTON AS INDICATED BY CHLOROPHYLL ESTIMATIONS

By W. R. G. Atkins, Sc.D., F.R.S. and Mary Parke, D.Sc.

From the Plymouth Laboratory

Introduction

When studying the suspended matter in sea water Armstrong & Atkins (1950) filtered carboys of sea water taken from the surface at the International Hydrographic Station, England No. 1, about 10 miles south-west of the Eddystone. The samples averaged 22 l., filtered through a Whatman No. 50 paper, 11 cm. diameter, on a Buchner funnel with the water pump. The first 10 l. was always re-filtered. The results for the suspended matter were shown to be only about 4% less than when filtration was through 'Gradocol' collodion membranes of average pore diameter 1·09 micron. The removal of the phytoplankton should thus be more complete than when the finest bolting silk is used, for according to Harvey (1945) the mesh apertures of the latter average $42 \times 50\,\mu$ when wet and swollen. Since there are many flagellates and non-motile forms less than $5\,\mu$ in length it is obvious that the net may let through much that is retained by the cellulose or collodion filters.

The suspended matter thus obtained gave us the opportunity of following the changes in the phytoplankton in the surface water, by extracting the pigments with acetone—a method introduced by Kreps & Verjbinskaya (1930), and by Harvey (1934*a*) with more accurate measurement of the volume filtered by the nets. Riley (1938–41) filtered surface samples through paper, as did Graham (1943). Krey at Kiel (1939) used 'cella'—presumably collodion—filters for water from 0–30 m. Cole & Jones (1949) also have made plankton counts using collodion filters.

Before proceeding it is appropriate to consider the known plastid pigments of the phytoplankton and their abundance in typical species.

The Plastid Pigments of the Phytoplankton

In recent years these have received much attention. According to Rabinowitch's summary (1945), the chlorophylls constitute about two-thirds of the total plastid pigments, the remaining third consisting of carotenoids, of which one-fifth contains orange red carotenes, polyene hydrocarbons, and four-fifths consists of their oxygen derivatives, namely yellowish xanthophylls. The amounts vary with species and environment, but the relative proportions are fairly constant in growing cultures. Chloroplasts often appear yellowish

or brown, rather than green, apparently due to the physical state of the plastid rather than to the preponderance of the yellow pigments.

According to Manning & Strain (1943), diatoms contain chlorophyll *a* and a little chlorophyll *c*, with carotenes and xanthophylls, mainly fucoxanthin, also diadinoxanthin and some diatoxanthin. The diatoms and brown algae have similar chlorophylls and xanthophylls. Pace (1941), however, did not find fucoxanthin in *Nitzschia closterium*, but it has been proved by Whitford (1947) to exist in the Chrysophycean *Phaeosphaera perforata*. Calculated on the dry weight of *Nitzschia closterium*, Pace found 2·17% chlorophyll *a* and 0·155% chlorophyll *b*, also β-carotene, cryptoxanthin, lutein, isolutein and two xanthophylls. The chlorophyll-carotenoid ratio was 3·77.

The presence of the xanthophylls and carotenes, and sometimes of other pigments, makes direct colorimetric comparisons useless for the estimation of the mixed chlorophylls. Of these, Strain (1949) summarizes the absorption-band measurements, and for chlorophyll *a*, $C_{55}H_{72}O_5N_4Mg$, reports principal bands at 440 and 660 mμ; for chlorophyll *b*, $C_{55}H_{70}O_6N_4Mg$—which may constitute 20–40% of the chlorophyll of the Chlorophyta—the bands are at 480 and 650. In red algae and diatoms, however, Manning & Strain (1943) found that *b* was less than 0·3% of *a*. The position of the bands varies somewhat according to the solvent used.

The formula and molecular structure of *c* is unknown, but it is found in small amounts along with chlorophyll *a* in diatoms, dinoflagellates and brown algae; the absorption maxima, in ether, are given as 446, 579·5 and 627 mμ (Strain, Manning & Hardin, 1944).

Chlorophyll *d* is found in very small amounts, with *a*, in red algae, though up to 25% is *d* in *Rhodochorton rothii*. It contains magnesium, but its formula is unknown. In ether its principal bands are at 445 and 686 mμ, and at about 457 and 698 mμ in methanol (Manning & Strain, 1943).

The Colorimetric Estimation of Chlorophyll and the Preparation of Extracts of Plastid Pigments from Phytoplankton

On viewing acetone solutions of a bought dry solid chlorophyll and of various extracts from algal cultures and sea water with a hand spectroscope, the absorption in the red gave a well-marked band. By inserting the Schott RG1 filter a spectrum of longer wave-length than 600 mμ is obtained, between which and the end of the visible red the band may reduce the light very markedly, and so permit of colorimetric comparisons without interference from the yellow pigments. A Kober colorimeter (by Klett) was used for this work.

There is, however, an uncertainty in the composition of chlorophyll powder, such as that from the British Drug Houses. Nettle leaves may be used as a

source. Though there are a number of chlorophylls and these have labile isomers the net effect of such changes as occur appears to be of no great importance as regards the absorption bands in the red; such small shifts in the bands would not seriously affect the colorimetric comparisons. Care should be taken to avoid errors due to evaporation of the acetone during the comparisons.

The aqueous acetone extracts from pure cultures of species selected from the phytoplankton (Parke, 1949) were thus compared among themselves and with chlorophyll standards. The cell numbers were counted in the haemocytometer field. Table 1 shows the numbers of algal cells from active cultures of measured average size which yield 1 mg. of chlorophyll.

The solvent used was of 'analytical reagent' quality and was added to the wet filter-paper on which the algal cells had been collected and washed with distilled water. If necessary, to keep in solution the salts of sea water liberated from the cells, a little distilled water was added till the cloudiness in the acetone vanished.

The chlorophyll-bearing cells, from cultures or from sea water, vary in size down even to one micron in diameter, as we have found recently. They are accordingly too small to be retained quantitatively on filter-paper, such as Whatman No. 42, intended for the finest precipitates. The filtration of large volumes on the 4 cm. diameter collodion membranes is very tedious and the membranes have to be changed frequently as they become choked. Centrifuging, even with tubes containing 250 ml. is unsatisfactory, and slow, though according to H. W. Harvey (private communication) dead cells are deposited better than are living. The simplest method is to add 5 ml. of a 1% solution of potassium aluminium sulphate crystals to about a litre of culture or sea water. The samples are usually at about pH 8, or over. The acid alum solution brings this nearer to neutrality; the reaction should be tested with bromthymol blue. If it is necessary to add more alum, for a very thick culture, the reaction may go slightly below neutrality, pH 7. If it is much below—in a fresh water—it can be restored by adding a little sodium bicarbonate. This is not done to precipitate the aluminium hydroxide which comes down from pH 3·5–5, but to avoid any possible effect of acid on the pigments. According to Atkins (1922) the reaction of algal cells is close to neutrality, whereas land plants are often markedly acid. Trouble arises more frequently in dense cultures through the reaction of the water being too alkaline, pH 9 or over. The aluminium does not then form a good floc, but either remains in solution or in a very fine suspension. The alkalinity may be reduced by passing in carbon dioxide, or by the cautious addition of very dilute acetic acid, till the pH is brought slightly below 7, and a yellowish green is given with bromthymol blue. This should be done before the addition of the alum solution, and it is advisable to allow the floc, with algae, to settle in weak light before filtration. It is often possible to pour off liquid over the floc, thus reducing time of filtration. Filtration

may then be effected on an 11 cm. Buchner funnel, with the filter pump. The rate should be low at first till the aluminium hydroxide floc has sealed the pores, when the suction may be increased. Unless too much alum has been added filtration proceeds at a reasonable rate. Algae from cultures are thus obtained for pigment studies, or it is possible to get the phytoplankton from 1 or 2 l. of sea water to follow the rate of production in the sea; smaller volumes should suffice when plankton is abundant.

Algae carried down in the transparent floc are readily seen under the microscope. *Dicrateria inornata* was perfectly visible and only by very careful adjustment of the light was it possible to discern the floc. Cells of *Chlamydomonas* were observed to be actively motile after two filtrations with too little alum or with too alkaline a solution for effective flocculation.

The weight of the aluminium hydroxide floc which is effective is amazingly small; a 1% solution of potassium aluminium sulphate crystals contains only 0·82 mg. of the hydroxide in 5 ml. Yet in 100 ml. of sea water this gives a marked turbidity in a few minutes and a sediment about 4 mm. in height in the measuring cylinder. Settling is naturally slower in a litre vessel, and as much as 15 ml., namely about 2·5 mg., may give with a culture a slowly filtering slime.

The chlorophyll content of pure algal cultures

A *Gymnodinium* culture contained 144 cells/mm.^{3}, (144 million/l.) The cell numbers per milligram of chlorophyll were obtained as follows. A freshly diluted chlorophyll solution contained 16·0 mg./l. Of this 50·0 matched 35·8 of a *Gymnodinium* extract, as read on the Kober scale, using filter RG1. The extract, therefore, contained 22·3 mg./l., and as its volume was 27·6 ml., which had been used in successive small portions to extract the algae filtered from 250 ml. of culture, the culture contained 2·46 mg./l., in 144 million cells. So 58·5 million cells contain 1·0 mg. The results for a number of species are given in Table I which include determinations on three species of diatom by Krey, Pace and Graham.

Differences in the volumes of the cells appear to account for the major differences in the milligram counts. One may not appreciate that, for example, the average volume of *Coscinodiscus centralis* is fourteen thousand times that of *Dicrateria inornata*.

To separate the pigments we tried aluminium oxide (Kahlbaum) specially prepared for such work. A blue green chlorophyll band was retained near the top; below this came one, or usually two, bands, orange red, and presumably carotenes. The liquid which came through was yellowish and appeared to be a xanthophyll, or several mixed perhaps. The above were obtained with the pigments in petroleum ether b.p. 40–60° C. after evaporation of the acetone on a water-bath. Whitford (1947) has reviewed previous work; he separated

the pigments on a starch column and with suitable solvent mixtures obtained bands for chlorophyll and two xanthophylls, the carotene coming through.

The separation of the chlorophylls can thus be readily effected and could be used as a check on the colorimetric comparison in the red.

TABLE I. NUMBER OF CELLS FROM ACTIVE ALGAL CULTURES WHICH YIELD 1 MG. OF CHLOROPHYLL. COLOUR REFERS TO EXTRACTS

	Size		Mg. count
	Mean (μ)	Range (μ)	
Chlorophyceae			
Order VOLVOCALES			
Chlamydomonas I, pure green. *By* F. Gross	10 × 5	8 × 4–12 × 6	202 × 10^6
Chlamydomonas III, pure green. *By* Mrs Föyn	8 × 6	6 × 4–12 × 8	109 × 10^6
Order CHLOROCOCCALES			
Chlorella I, yellowish green	3·5*d*	2·5–4·5*d*	2400 × 10^6
Chrysophyceae			
Order CHRYSOMONADALES			
Dicrateria inornata Parke, yellowish green	4*d*	3–5·5*d*	563 × 10^6
Bacillariophyceae			
Order CENTRALES			
Coscinodiscus centralis Ehr., yellowish green. *By* R. Bainbridge	110*d* × 50*t*	105*d* × 35*t* 140*d* × 60*t*	74 × 10^3
Chaetoceros gracilis Schütt (Krey, 1939)	8 × 6*b*	—	286 × 10^3
C. vanheurckii Gran (Graham, 1943)	24–28*w*	—	170 × 10^3
Thalassiosira gravida Cleve, yellowish green	22*d* × 12*t*	20*d* × 10*t*–25 × 14	123 × 10^6
Order PENNALES			
Nitzschia closterium (Ehr.) W.Sm. forma *minutissima*. *By* Allen and Nelson; pure green	30 × 3–8 × 3*b*	25 × 3–35 × 4	743 × 10^6
N. seriata Cleve (Pace, 1941)	100 × 6	—	1·25 × 10^6
Cryptophyceae			
Order CRYPTOMONADALES			
Hemiselmis rufescens Parke, almost pure green with insoluble red	7 × 4 × 3	4 × 3·5 × 2–8·5 × 5 × 3	3260 × 10^6
Dinophyceae			
Order DINOFLAGELLATA			
Gymnodinium sp. very close to *G. simplex*, yellowish green	15*	10–22	58 × 10^6

Notes: *b*, body, without spines; *d*, diameter; *t*, thickness; *w*, width of cell; * sphaeroidal; *By*, isolated by and maintained since at Plymouth.

THE SEASONAL CHANGES IN THE PHYTOPLANKTON

These have for many years been studied by the changes in concentration of phosphate and other nutrient salts. A number of isolated measurements have been made, as mentioned previously, but Harvey (1934*b*) followed the changes at a station, L 4, inside the Eddystone using a net filtering measured volumes of water and an arbitrary colorimetric scale compounded with potassium chromate and crystalline nickel sulphate.

There is, however, an uncertainty in the number of molecules of water of crystallization even in the 'analytical reagent' quality. The figure is between $6H_2O$, taken by Harvey, and $7H_2O$. The uncertainty is 6%. A solution of

known nickel content may, however, be prepared by dissolving nickel wire. The nickel chromate standards have been considered to be a tolerably good colour match for acetone extracts of plankton. We are indebted to Dr Harvey for kindly comparing an extract from plankton filtered from a carboy taken on 30 November 1949 (Table II). This he assessed as corresponding to 10–15 units in 10 ml., but the extract was far more yellow than the standard, so a closer match was not possible. Viewing the tubes through the filter RG 1, the sample was rather under 8 units, possibly as low as 6 units. Taking into account the volumes of extract and of water this corresponds to 1·39–1·04 mg. of chlorophyll/m.^{3}, using Harvey's value, based on Guthrie's work, of 0·3 μg. of chlorophyll/unit. The result found by comparison with a chlorophyll standard with the RG 1 filter was 1·43 mg./m.^{3}. It seems possible that the yellower colour of the November extract may have been due to the presence of a larger number of flagellates than are ordinarily found in the net plankton to estimate which the colour units were devised.

Riley (1938) estimated chlorophyll from algae by comparison with a chlorophyll prepared by Dr C. G. Deuber of Yale. He separated the chlorophyll from the yellow pigments by saponifying it and removing the carotenoids in ethyl ether. He found 1 unit of the Harvey scale to correspond to 0·88 $\pm$ 0·01 μg. chlorophyll. There was good agreement between the dry organic matter and the chlorophyll content, but only in the upper layers of the water. Paper filtration (Whatman No. 44) was found to give up to seven times as much chlorophyll extract as did bolting silk, and use of collodion membrane produced about 6% more than did paper in Long Island Sound (1941 *a*). Using the same method for removing the yellow pigments Riley tabulated Harvey units against chlorophyll for his Long Island work and the mean showed 0·26 μg./unit. This is much below his earlier value, but agrees tolerably well with Harvey's estimated value 0·3 μg., which seems to accord reasonably well with the single comparison already quoted in this paper when the red filter was used. Riley also records that 17·44 mg. chlorophyll corresponded to 600 mg. dry organic matter, namely the chlorophyll was 2·91%. This is close to Pace's value 2·32% for the sum of chlorophyll *a* and *b* in *Nitzschia closterium*, in which a lower value is to be expected as the analysis refers to a silica-bearing organism only.

The extracts made during 1948 and 1949 from suspended matter filtered on collodion from water from Station E 1 (which was selected to be beyond the range of fluctuation due to land drainage) were compared among themselves without the red filter and, using the filter, with chlorophyll solutions of suitable strength. The results are shown in Table II, together with the sea temperature, the suspended inorganic matter and ash after incineration (S.I.M.A.) and the percentage of silica contained in the latter, in order to see whether any relation existed between these and high chlorophyll values. No such relation is, however, observable. Thus 2020 and 1190 mg./m.^{3} S.I.M.A. both have 44%

of silica and correspond respectively to 1·05 and 1·43 mg. of chlorophyll/m.³. Furthermore, 490 mg./m.³ S.I.M.A. had 43% of silica, but only 0·17 mg./m.³ of chlorophyll.

In 1948 the chlorophyll content was much as would be expected from the phosphate studies, with a well-marked maximum in April, and a lesser crest in October, separated by the year's minimum in mid-August. As always, a larger number of observations would have been better. For 1949 the April figure observed was only half that of 1948, but this was, after a drop, followed by a large outburst in June and a high maximum in July, leading, after fluctuations to a late November outburst rather greater than that observed in April. It must be remembered, however, that these observations are on

TABLE II. CHLOROPHYLL CONTENT, WITH ACCOMPANYING SURFACE TEMPERATURE, SUSPENDED INORGANIC MATTER AND ASH (S.I.M.A.), AND SILICA CONTENT OF THE LATTER

Chlorophyll and S.I.M.A in mg./m.³ sea water (parts per thousand million). Silica in percentage of S.I.M.A.

Date 1948	Chlorophyll	°C	S.I.M.A.	SiO_2%	Date 1949	Chlorophyll	°C	S.I.M.A.	SiO_2%
Jan.	—	—	—	—	5 Jan.	0·61	11·2	760	21
11 Feb.	—	10·1	—	—	1 Feb.	0·86	10·2	1600	26
10 Mar.	0·92	9·3	—	—	1 Mar.	0·58	10·1	740	21
12 Apr.	2·84	10·2	—	—	13 Apr.	1·37	9·9	800	37
10 May	—	12·4	—	—	9 May	0·57	11·5	800	31
9 June	0·73	12·6	1140	54	9 June	3·40	13·9	1360	52
15 July	0·82	14·7	2770*	25	8 July	4·30	16·5	1880	41
Aug.	—	—	—	—	8 Aug.	0·36	15·3	450	18
16 Aug.	0·17	15·4	890	43	17 Aug.	1·05	16·0	2020	44
31 Aug.	—	16·8	—	—	29 Aug.	0·51	19·4	800	42
4 Oct.	1·22	14·7	490	44	6 Oct.	—	16·4	590	43
30 Nov.	0·30	13·2	950	17	8 Nov.	1·43	14·0	1190	44

* 70% of this was calcium carbonate probably precipitated out of the water.

surface water and there is now evidence from several sources that the surface is the seat of a large amount of suspended matter. None the less, the surface outbursts in June and July are remarkable.

When these figures 0·17–4·3 mg./m.³ chlorophyll are compared with values recorded by other workers, it is better to neglect the early net-filtered results, which are clearly low. The numerous measurements by Riley, filtering through the finest paper, would be low if the small flagellates were an important constituent. For surface samples from the North Atlantic he gives (1939) as mean 1·2 and maximum 3·6 mg./m.³, with 5·6 and 27·2 for George's Bank (1941*b*) also 17·4 and 62·0 for Long Island Sound. Riley has recently (1949) given an extensive review of the subject. For La Jolla, Graham (1943) gives 0·77 and 1·86 maximum. His results appear to be low, as he reports no chlorophyll found in a sample in which *N. seriata* constituted 83% of the catch. His method of estimating the chlorophyll avoids errors due to the yellow pigments, for he used a visual spectrophotometer set at 668 mμ. with slit width

0·4 mm. Krey (1939) used a 'cella' (collodion) filter and for 0–30 m. at Kiel got a mean of 2·00 mg./m.^{3} and a maximum of 5·00.

It has been customary for biologists to count microscopic organisms on the ruled squares of the Thoma haemocytometer, the side of the ruled area being 1 mm. and the depth one-tenth thereof. The volume is one-tenth of a cubic millimetre. It may serve to show how sparsely populated sea water is by recalling that the simultaneous utilization of all the phosphate present at the winter maximum in the English Channel suffices to produce *N. closterium* at a density of 2·7 per haemocytometer field (Atkins, 1923). One milligram of phosphorus suffices for 2050×10^6 cells of *N. closterium* var. *minutissima*. When compared with the production of 743×10^6 cells for 1 mg. of chlorophyll (Table I) we see that the chlorophyll to phosphorus ratio is 2·76 in this species, weight for weight.

Table III. Number of Cells in a Haemocytometer Field Derivable from the Observed Maximum 4·3 mg. of Chlorophyll per Cubic Metre, Assuming all to be of one Species as Listed

Species	Cells per field
Coscinodiscus centralis	$0{\cdot}32 \times 10^{-4}$
Thalassiosira gravida	0·053
Nitzschia closterium var. *minutissima*	0·32
Dicrateria inornata	0·24
Isochrysis galbana	0·27
Hemiselmis rufescens	1·40
Chlamydomonas I	0·087
Chlamydomonas II	0·047
Chlorella I	1·03
Gymnodinium sp.	0·025
Human red blood corpuscles	450×10^3

Table III shows the number of cells per field which would be produced if the maximum amount of chlorophyll recorded in Table II, namely 4·30 mg./m.^{3}, were all produced by the single species listed. It may be seen that, for *Nitzschia*, the observed maximum is only about one-eighth of the possible, were the winter maximum of phosphorus to give one crop without any intermediate grazing down; thus in a pure culture the chlorophyll produced by water of this composition would be about $4{\cdot}3 \times 8{\cdot}4$, namely 36 mg./cm.^{3}.

The figures in the Table indicate the difficulty of making direct counts.

Summary

The pigments of pure cultures of algae, of known number per volume, have been extracted with aqueous acetone after separation by filtration. The extracts were compared in a Kober colorimeter with standard solutions of a preparation of bought chlorophyll. The number required to give 1 mg. of chlorophyll was thus determined.

The algae studied included: Chlorophyceae, two species of *Chlamydomonas* and one *Chlorella* not yet described; Chrysophyceae, *Dicrateria*

inornata Parke; Bacillariophyceae, *Coscinodiscus centralis* Ehr., *Thalassiosira gravida* Cleve and *Nitzschia closterium* (Ehr.) W.Sm. forma *minutissima*; Cryptophyceae, *Hemiselmis rufescens* Parke; Dinophyceae, *Gymnodinium* sp. The numbers per milligram of chlorophyll varied from 74×10^3 for *Coscinodiscus* to over 3200×10^6 for *Hemiselmis rufescens*. Of the nine cultures, six were between 50 and 750×10^6. The volume of the cell is the decisive factor in the milligram count.

Filtration of these and of sea-water samples was made through either collodion membranes of known average pore diameter, supplied by courtesy of the Director of the Department of Pathology, St Mary's Hospital, London, or through the finest grade of Whatman filter-paper. To retain the algal cells on paper about 5 ml. of a 1% solution of alum was added. The transparent floc serves to entangle the cells. They are thus ready for examination under the microscope, and motile organisms are slowed down or brought to rest. The floc will settle down in a cylinder. The water should be close to pH 7 before addition of the alum.

Colorimetric estimation of chlorophyll can be made even with extracts which are yellowish green or yellow by using a red colour filter Schott RG1 cutting off close to 0·6 μ, which is placed over the eyepiece of the colorimeter.

The seasonal changes in the chlorophyll content of water in the English Channel, about 20 miles off Plymouth, were followed from March 1948 to November 1949 inclusive, by filtering surface water. The spring maxima in April were respectively 2·84 and 1·37 mg./m.^{3}, and the autumn maxima 1·22 and 1·43. The yearly minima were in August, 0·17 and 0·36. But most unexpectedly June and July 1949 gave 3·40 and 4·30 respectively. Such figures are comparable with those of Krey, for Kiel, 2 mg. mean and 5 mg. maximum, and of Riley, for North Atlantic, 1·2 mean and 3·6 maximum.

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THE BIOLOGY OF *ASTERIAS RUBENS* L. II. PARASITIZATION OF THE GONADS BY THE CILIATE *ORCHITOPHRYA STELLARUM* CÉPÈDE

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(Plate I)

CONTENTS

	PAGE
Introduction	619
Distribution of the Parasite off Plymouth	619
Distribution of the Parasite within the Host	621
Effect of the Parasite on the Testes of *Asterias rubens*	622
Discussion	623
Summary	624
References	624

Introduction

The astomatous holotrich ciliate, *Orchitophrya stellarum*, was originally described and named by Cépède (1907*a*, *b*), who found it in the gonads of only three males out of a total of over 6000 *Asterias rubens* of both sexes. These starfishes were taken by him from the Boulogne and Wimereux area. There was no trace of the parasite in any ovaries, but he noticed that it caused a partial and direct castration of its male host. *Orchitophrya* was found by Piatt (1935) in the testes of *Asterias forbesi* in Long Island Sound, where Burrows (1936) observed that the percentage of parasitized males varied from 1 to 20% according to the locality. Burrows also found that a small number of the female starfishes (about 1%) were infected. Smith (1936) recorded the parasite in the ovaries of about 25% of the females of *A. vulgaris* from oyster beds in Malpeque Bay, Prince Edward Island. Eggs taken from these infected ovaries appeared normal and were fertilizable.

I am indebted to Mr Y. R. Tripathi for assistance in the original identification of the parasite, and to Dr J. S. Alexandrowicz for making the photomicrographs.

Distribution of the Parasite off Plymouth

During the years 1946–50 large numbers of *A. rubens* have been trawled from different localities in the Plymouth area. In the course of investigations on the reproductive cycle in these localized populations, smears have been taken

from the gonads of each starfish and transverse sections cut of a number of selected gonads. In March 1947 trawling was commenced on the Outer Grounds, to the south and south-west of Eddystone. The differences between the starfish from this area and those from the more northerly Rame-Eddystone Grounds have already been described (Vevers, 1949). *Orchitophrya stellarum* was found in a varying percentage of the males from all the six trawl hauls taken in spring 1947 on the Outer Grounds. In the early months of the years 1948, 1949 and 1950 the parasite was again found in male starfishes from these Grounds and also in a population of *Asterias rubens* trawled from Asia Shoal, Plymouth Sound. The parasite has never been found in starfishes from the geographically intermediate Rame-Eddystone Grounds. The significance of this

TABLE I. ANALYSIS OF PARASITE OCCURRENCES IN STARFISH FROM HAULS FROM OUTER GROUNDS AND PLYMOUTH SOUND

Date	Total in haul	Total males	No. of males parasitized	Approx. percentage of males parasitized
	(*a*) Outer Grounds			
20. iii. 47	33	12	3	25
9. iv. 47	29	11	3	27
17. iv. 47	44	17	4	24
18. iv. 47	50	25	7	28
25. iv. 47	175	66	16	24
23. v. 47	57	17	2	12
15. i. 48	29	15	1	7
12. iii. 48	38	15	1	7
14. iv. 48	103	50	6	12
13. v. 48	231	87	1	1
10. ii. 49	63	26	2	8
15. iii. 49	46	17	1	6
14. ii. 50	41	23	2	9
9. iii. 50	79	32	3	10
	(*b*) Plymouth Sound (Asia Shoal)			
16. iv. 48	100	52	3	6
20. iv. 49	25	10	1	10
10. iii. 50	80	37	1	3

distribution will be discussed later. Table I gives a synopsis of the occurrences of *Orchitophrya stellarum* in *Asterias rubens* from the Plymouth area.

The occurrence of the parasite is strictly seasonal. It has only been found near Plymouth during January to May (inclusive) when the host's testes are either ripe or nearly ripe. Smith (1936) and Burrows (1936) both record it as occurring during 'summer'.

The absolute number of parasitized starfishes caught in any one haul is necessarily small and so it is difficult to obtain a figure representing the true percentage of males infected. However, the data given in Table I show clearly that the percentage infected was much greater in 1947 than in any of the three succeeding years. The catches taken from the Outer Grounds in March and April 1947 gave very constant percentages of infected males. A month later

(23 May 1947) the percentage infected had dropped to half; probably because most of the males had spawned in the meantime, leaving fewer ripening testes available for the parasites. In January-April 1948 the percentage infected was, on the average, 10, and again there was a sharp drop in percentage to less than 2 in May. There were only two infected catches in 1949 from the Outer Grounds, one in February and one in March, and the percentage with parasites was less than 10. The same was found in the two catches for 1950.

In the Plymouth Sound starfish population *Orchitophrya* has been found only in small numbers in one catch in each of the years 1948, 1949 and 1950.

The percentage of males infected was proportionately much greater in the size classes 10·0–19·9 cm. than in the size classes 5·0–9·9 cm. and 20·0–25·9 cm. (Table II). In the lower-size classes (5·0–9·9 cm.) the scarcity of parasitized individuals is understandable, since some, at least, of these starfishes were definitely juvenile with testes which showed no signs of ripening at the time of observation.

Table II. Size Distribution of Infected Males in the Population (Outer Grounds)

Size class in cm.	Total males	Infected males	Percentage infected
5·0–9·9	35	2	6
10·0–14·9	162	29	18
15·0–19·9	181	19	11
20·0–25·9	35	1	3

The very low percentage of infections in the highest size classes (20·0–25·9 cm.) suggests that there may be a certain resistance to the parasites with increased host size. There is, however, no direct evidence for this interpretation.

Distribution of the Parasite within the Host

Burrows (1936) noted variation in the amount of parasites within the individual, including cases where some gonads were parasitized and others were normal. Similar conditions were found in the present investigation, thus in starfish 3076 (16 April 1948) there was a very heavy infection of the testes in arm II/interradius 2/3, while all the rest of the testes showed mobile spermatozoa and no parasites. In starfish 3087 (16 April 1948) there were medium infections in two testes in non-contiguous arms and no parasites in the other eight gonads. At the time these starfishes were caught, in mid-April, most of the starfishes on the Outer Grounds were ripe, but few had spawned. In the previous year larger catches of starfishes were made, and among these were a few in which ripe, spawned and parasitized testes were

found in the same animal. Thus in starfish 998 (23 May 1947) the condition of the gonads was:

Arm	Interradius	Condition of gonad
I	5/1	Spawned, re-ripening
	1/2	Spawned
II	Arm missing	
III	2/3	Spawned
	3/4	Mobile sperm distally, rest spawned
IV	3/4	Few parasites
	4/5	Few parasites
V	4/5	Mobile sperm distally, rest spawned
	5/1	Spawned

There is no doubt that the main centre of infection is in the testes, although the parasites can sometimes be found in other organs. In starfish 640, for instance, *Orchitophrya* was found in the gut and coelomic fluid as well as in the testes, but not in the digestive coeca or tube feet. These are probably chance infections from lesions in the testis and are not considered to be of any importance.

Effect of the Parasite on the Testes of *Asterias rubens*

Cépède (1910) gives a good description of the morphology and life cycle of the parasite, and he noted that it caused partial or direct castration of the host. His material was very limited and neither he nor subsequent workers have recorded the histological changes which occur in testes infected with *Orchitophrya*. With the large number of infected males available from the Plymouth grounds, it has now been possible to obtain further information on this subject.

In the early stages of infection the testes still have well developed spermatogonial ridges, with numerous spermatocytes and spermatids filling the lumen of each tubule. As the parasites increase in number, the sexual products in the lumen disappear and a transverse section then shows that each tubule has distinct spermatogonial ridges and its lumen is filled with parasites. The ridges become progressively smaller and the parasites increasingly crowded (Pl. I, fig. 1). The nutrient medium in which the parasites are living is that of the ripening germ cells, and as the latter disappear so does the food supply of the parasites. When this happens the parasites start to decrease in numbers and the gonad tubules show only a very thin layer of genital epithelium (Pl. I, figs. 2 and 4). In this stage the connective tissue sheath begins to thicken, probably due to a shrinking of the whole tubule, as it becomes less distended with parasites.

Finally, very few parasites are left in the tubule lumina, there is little or no trace of genital epithelium and all that remains are the thick shrunken sheaths of the original testis tubules (Pl. I, fig. 3).

Discussion

The spread of the parasite would appear to be greater in starfish populations which are relatively crowded, for the largest percentages of infected males occurred on the Outer Grounds in 1947. During this year the number of starfishes caught on these grounds in comparable hauls was larger than in subsequent years, and in addition the values for their mean individual body and testes sizes and available food supply were also higher. It has already been found (Vevers, 1949) that a numerically rich population, with abundant food supply, has a large mean body and gonad size. From the present observations it appears that rich and 'successful' populations (as on the Outer Grounds and on Asia Shoal, Plymouth Sound) were also characterized by the presence of a varying percentage of males with ciliate-infected testes. Conversely, a starfish population with small numbers, and low mean body and gonad size (as on the Rame-Eddystone Grounds) showed no trace of the parasites, although many starfishes from these grounds were examined.

Testes containing *Orchitophrya* never showed mobile sperms, even when the infection was relatively light, and there is little doubt that once it has been infected a testis ceases to function as a reproductive organ during that season. Although sometimes ripe, spawned and infected testes were found in the same starfish, it was more common to find all the testes of a starfish infected in some degree. In a population where over 20% of the males were infected (as in the Outer Grounds in March-April 1947) the intensity of reproduction, measured as the number of potential gametes, would necessarily be reduced by at least a similar amount, since the same number of predators and adverse factors would be preying on a reduced number of gametes. On theoretical grounds this check to reproduction should be reflected in a reduced population in subsequent years. There was, in fact, an observed reduction in the population of *Asterias rubens* on the Outer Grounds in 1948, 1949 and 1950 as compared with 1947 (Vevers, unpublished data). As it is not possible to follow the fate of broods which go through a pelagic phase one cannot gather direct evidence to show the causes of such a population reduction. On the Outer Grounds any reduction in population following on a year of heavy testis parasitization could easily be masked by immigration from neighbouring areas. There are also other factors, such as movement of food supply, which might reduce the population in numbers and mean body size. The observed population reduction since 1947 is probably the result of many factors, but it is considered that the parasitic castration of over 20% of the males in this population during 1947 must have played a definite part, and that it did, in practice, act as a natural check to a crowded population, a view which is supported by the observations of Galtsoff & Loosanoff (1939) on *A. forbesi*.

Summary

The parasitic astomatous holotrich ciliate, *Orchitophrya stellarum* Cépède, has been found in the testes of starfishes (*Asterias rubens*) in the Plymouth area. It was found only in starfishes from numerically rich and well-fed populations, which also showed large gonad growth. In such populations it occurred in up to 28% of the males during March-April 1947, and in lower percentages during the spring of the three following years. The parasite was never found in a geographically adjacent population containing smaller numbers of poorly fed starfishes. The parasite was found to be relatively more common in the testes of medium-sized starfishes than in those of large and small starfishes.

Presence of the parasite causes a complete breakdown of all the germinal tissue of the testes, so that most of the infected starfishes suffer complete castration. This involution of the testicular tissue has been studied, and photomicrographs are given which show a number of stages in the process.

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EXPLANATION OF PLATE I

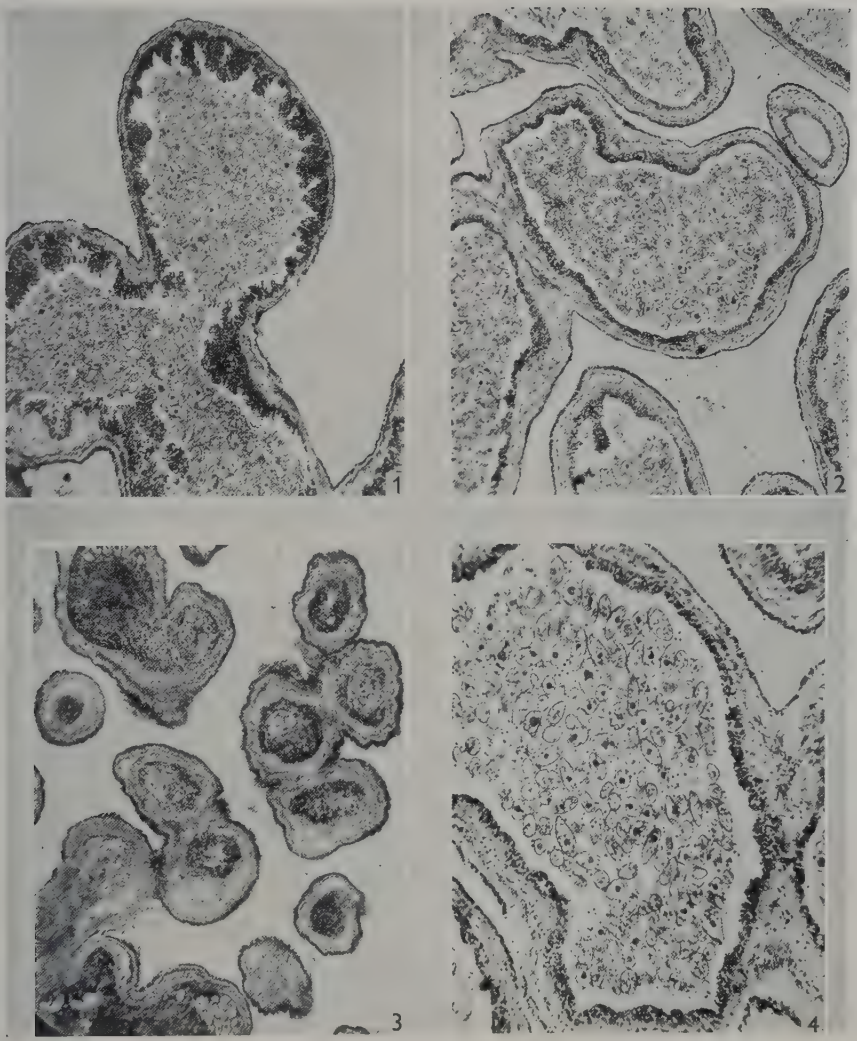
Photomicrographs of transverse sections of *Asterias rubens* testes showing stages of infection by *Orchitophrya stellarum*.

Fig. 1. Numerous parasites free in the lumen of a gonad tubule. Spermatogonial ridges still distinct.

Fig. 2. Parasites starting to decrease; spermatogonial ridges have disappeared.

Fig. 3. Final stage in the involution of the testis, with genital epithelium destroyed and gonad only represented by the thick shrunken connective tissue sheath. Very few parasites remain.

Fig. 4. Enlargement of part of fig. 2 to show parasites (cut at different angles) completely filling the lumen of the testis tubule. Very few germinal cells remain among the parasites.



Figs. 1–4.

OBSERVATIONS ON THE SPAWNING BEHAVIOUR OF *SACCOGLOSSUS HORSTI* BRAMBELL & GOODHART, AND OF OTHER ENTEROPNEUSTA

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CONTENTS

	PAGE
Introduction	625
Habitat of *Saccoglossus*	626
Field observations on *Saccoglossus horsti*	
Spawning of females	627
Spawning of males	628
Fertilization	628
Mechanism of spawning	629
Laboratory observations on *S. horsti*	630
Breeding season of *Saccoglossus horsti* and *Saccoglossus cambrensis*	632
Discussion	635
Summary	636
References	637

Introduction

A survey of the literature reveals few observations on the spawning behaviour of the Enteropneusta. Those existing are confined to descriptions of various continental species.

Bateson (1884, 1886) suggested that *Saccoglossus kowalevskyi* Agassiz from Chesapeake Bay released its sperm and ova by a rupturing of the body wall, the former dehiscing as lobate spermatophoric masses. Ritter & Davis (1904) studied *S. pusillus* Ritter at San Pedro, California, and stated that 'sperm is discharged in a delicate milky stream through the pores of the ripe genital lobes', and similarly the ova. They discovered eggs and embryos within a burrow, and concluded that that was their normal place of release and development. Davis (1908) collected all his material for a study of the embryology of *S. pusillus* from the burrows. Heider (1909) recorded a clump of eggs of *Balanoglossus clavigerus* Delle Chiaje amongst specimens received from Grado. Stiasny (1913) also worked on this species, and made observations on the method of spawning, fertilization and breeding season. A spawning male specimen of *Glossobalanus marginatus* was described by Meek (1922). This had been dredged from a depth of 52 fm. off the Farne Islands in the North Sea. Dawydoff (1928) described the egg masses of *Glossobalanus minutus* Kowalevsky at Naples. Laboratory records were made at Tortugas by Payne (1936) for *Ptychodera bahamensis* Spengel. Probably the most complete account of

spawning as yet recorded, for any species, is that of Kirk (1937, 1938), for *Saccoglossus otagoensis* Benham, found near Wellington, N.Z. This is a rock-pool inhabitant, and has a comparatively specialized mode of spawning. During their study of *S. pygmaeus*, Hinrichs & Jacobi (1938) noted some fertilized eggs in their aquaria, but they did not give many details.

The recent discovery of *S. cambrensis* in the Menai Straits (Brambell & Cole, 1939), and *S. horsti* in the Solent (Brambell & Goodhart, 1941), provided an opportunity for a study of their development. The spawning behaviour will be dealt with here, and the development described in subsequent papers. The following account is, in the main, confined to *S. horsti* on which the majority of the observations were made, with appropriate references to other species.

I am greatly indebted to Prof. F. W. Rogers Brambell, F.R.S., and Dr T. B. Reynoldson, of the Department of Zoology, University College of North Wales, for their continued interest and encouragement throughout this work. Also to Dr E. W. Knight Jones of the Marine Biological Station, University College of North Wales, and Prof. J. E. G. Raymont of the Department of Zoology, The University College of Southampton, whose information concerning the Solent grounds greatly facilitated the collection of material. These collections, and others referred to in the text, were made possible by a grant from the Browne Research Fund of the Royal Society. The air and sea temperatures quoted for the Southampton area were very kindly provided by Lieut.-Commander D. H. Macmillan, R.N.R., Hydrographic Surveyor to the Southampton Harbour Board.

Habitat of *Saccoglossus*

S. horsti was originally described as occurring in deep grey mud, of a glutinous type, from just above low-water mark spring tides to a little way above low-water mark neap tides. Subsequent exploration of the Solent area revealed a marked preference for areas of comparatively clean sand containing a smaller proportion of clay, silt, organic carbon and shell debris than was given in the original analysis. Such areas were invariably saturated, the water table lying above, or immediately below the surface of the sand. Shallow pools and streams of drainage water from neighbouring beds of *Spartina townshendii* Groves, and the upper reaches of the shore helped to maintain this saturated condition during the ebb tide. Regions were noted, however, where the water table was often 6 in. below the surface at the time of extreme low water. Surface casts and holes indicated that the number of specimens in these comparatively dry areas was less than in the others. A substrate of gravel, comparable to that so characteristic of the *Saccoglossus cambrensis* beds, was noted in many well-populated regions of the shore.

The animals live in reasonably well defined, irregularly coiled burrows, lined with mucus, and extending 4–8 in. below the surface.

Field Observations on *Saccoglossus horsti*

Spawning of Females

Collections were made on the Solent beds during all the workable tides of June 1946, May 1947, 1948, 1949 and May–June 1950, but it was not until the last two years that any spawning was observed in the field.

The area worked during these years covered several acres of the shore, and surface casts averaging over 500 per m.^{2} were common in the more densely populated parts. Observations were made throughout every tide during the period 12–16 May 1949, 28 May–2 June 1950 inclusive. On both occasions ripe adults were extremely abundant and extraordinarily difficult to remove from their burrows without damaging them. Such pronounced ripeness had not been encountered in previous years. The condition was general.

Whilst making field notes on the evening ebb of 15 May 1949, the first indications of spawning were observed. Particles of detritus had been seen passing in a constant stream into a burrow, when the continuity of the flow was interrupted, became spasmodic, and was finally reversed. Detrital material which had just passed into the burrow was expelled. Almost immediately after this, a continuous flow of viscous, perfectly transparent mucus was seen to be exuding slowly from the burrow. Its refractive index was such as to make it almost invisible under the overlying water, but the movement of sand particles and detritus around its margin and settling on it from above indicated its shape and movement. When it first appeared this mucus was too viscous to be drawn up into a pipette of 1·5 mm. bore, but it became progressively less viscous after a period of exposure to the surrounding water. Light grey ovoid eggs then began to appear, embedded in a 'mucus cord', which coiled upon itself around the mouth of the burrow. The eggs were sparse at first, but soon the mucus cord was uniformly speckled with them. The cord was about 3 mm. in diameter, the eggs about 0·25 mm. and spaced roughly 0·5 mm. apart. Occasionally they lay in rows 4 or 5 deep, but this arrangement was rapidly destroyed as the cord coiled upon itself and adjacent portions tended to fuse. The production of the egg mass usually went on steadily for 5–10 min., but sometimes it was rather erratic and more prolonged. The grey colour of the egg masses made them easily visible against the yellow of the sand. Spawning commenced about 30 min. after the shore had been exposed by the receding tide. Within an hour the entire bed was 'splashed' with egg masses, each some 7–8 cm.^{2} in area. The number of specimens spawning at a time increased to a maximum during this period, and then gradually decreased. After 2 hr., the rate of production of new egg masses had declined considerably, and within 2½ hr. there was no evidence of any being formed. Although no accurate counts were possible in the field, it was estimated that each egg mass contained some 2500–3000 eggs. These were contained in cords some 15–20 cm. long. Extension of the cord was, however, impossible, for the overlapping coils adhered tenaciously to

each other immediately on contact, and the whole mass coalesced within minutes of its formation. The resultant mass resembled miniature frog's spawn in many respects, notably in its elastic and slippery nature, a property which made collection extremely difficult.

Spawning of males

Approximately 20 min. after the first egg mass was seen, pale pink and milky white blotches began to appear amongst them. These were dense clouds of sperms issuing from the burrows of the males in much the same manner as that described for the eggs. The enveloping mucus was, however, less viscous, and in consequence the sperm clouds were slowly carried away and dispersed by the currents in the overlying water. These blotches, at first some 20–30 cm.^{2} in area, thus became thin streaks of pink or milky translucency, and extended for 30–40 cm. from the burrow mouth before becoming so diffuse as to be invisible to the naked eye.

These observations are similar to those recently made by Newell (1948) on *Arenicola marina L.*

Although the area where this spawning took place had been carefully scrutinized for the entire period of its exposure during the morning and evening ebbs of the previous seven tides, and the subsequent one, the phenomenon was not repeated. Neither was there any evidence of it when the shore was examined during the ebb on the following morning.

Fertilization

Egg masses in the immediate vicinity of the sperm clouds erected their fertilization membranes rapidly, thereby increasing their diameter fourfold. Others, apparently upstream and beyond the visible range of dispersal of the sperms, also showed signs of fertilization, suggesting that it was not wholly dependent on the currents in the overlying water.

The process of fertilization was accompanied by a gradual reduction in viscosity of the enveloping mucus as it was dissociated by the surrounding medium. Whereas there was evidence of disintegration of the egg mass prior to the fertilization of its constituents, there was no doubt that dissociation of the enveloping mucus took place rapidly once the fertilization membranes had been erected. The outermost eggs were fertilized first and soon detached themselves from the underlying ones. This process continued until the entire mass had been fertilized, and the eggs had been carried away by the currents in the overlying water, or remained in a loose cluster around the mouth of the burrow, to be subsequently dispersed by the incoming tide.

Partially fertilized egg masses, with the fertilized eggs as yet undetached, were observed in the direct flow of the sperms from the burrows. Such egg

masses were pink or white with sperms, but the preponderance of male elements did not seem to affect the normal progress of fertilization and erection of membranes of the unfertilized eggs. Whereas the unfertilized eggs released by dissociation of the enveloping mucus either lay in crevices amongst the sand grains, or were slowly rolled away by the over-running stream, the more buoyant fertilized ones were carried away without any difficulty. This indicated that the specific gravity of the latter had been considerably reduced by the erection of their fertilization membranes. Crude artificial fertilizations carried out with freshly spawned eggs and sperm, in the field, indicated the existence of a maturation period comparable to that noted in the laboratory. The eggs were placed in about 500 c.c. of clean sea water in a collecting jar, and a few drops of sperm added. After gentle stirring they were allowed to stand undisturbed for 30 min. When examined at the end of this period few of the eggs had been fertilized, but on further examination after an hour had elapsed the majority of the eggs had erected their fertilization membranes. These eggs remained in almost permanent suspension in the water when disturbed by stirring. The few remaining, unfertilized eggs settled rapidly. Although no control was possible under the circumstances, it seemed fairly certain that the eggs were impregnated by the sperms added, and not by any already present in the water.

Mechanism of Spawning

Since it was not possible to see the animals spawning, except for occasional glimpses of a proboscis at the burrow mouth, the behaviour of the animals during this period must be deduced from the way the genital products are forced out on to the surface.

The gradual outflow of detritus from the burrow prior to the appearance of mucus and, subsequently, of eggs or sperms, indicates a movement of the occupant towards the surface preparatory to spawning. The mucous glands secrete a larger quantity of mucus than usual. Probably the collar contributes a high proportion of the mucus, assisted by the large clusters of glandular cells in the genital and post-genital regions. When the release of the eggs and sperms has begun the animal is thought to retreat slowly to the lower regions of the burrow, continuing to produce large quantities of mucus, and spawning as it does so. After a short period the movement is reversed, and the animal now proceeds to force the mucus along with the enveloped eggs or sperm out of the burrow. This would explain the initial smooth outflow of the mucus cord from the burrow. Eggs and sperms were absent from the first few centimetres of this, possibly because the mucus comprising them was produced by the regions anterior to the gonads, viz. the proboscis, collar and the anterior branchial region of the trunk. The slow rhythmic flowing of the cord, referred to earlier, was probably due to the worm repeating the process. The even rather than patchy distribution of the sexual elements within the mucus indicates that

they are released in an orderly manner and not cataclysmically. This suggests release through the genital pores, rather than by a rupturing of the body wall, a suggestion supported by the absence of evidence of disintegration in any spent specimens examined.

Complete discharge of the genital products does not take place, since the ovaries of adults always contain some large eggs. Specimens might thus spawn more than once in a season. Some were noted where the gonads were asymmetrically placed, an arrangement which might be due to one side discharging its products before the other. The remarkable synchronization between the times of release of the female and male elements indicated that this was an instance of induced spawning. Similar instances of induced spawning have been quoted, and described by Thorson (1946). Whereas the literature revealed the rule that ripe females of various invertebrates will not spawn unless induced to do so by the presence of the active sperm of their own species, the ripe females of *Saccoglossus horsti* spawned first, and seemed to induce the males to spawn. Other marine animals have been known to behave in a similar manner, e.g. *Perinereis marionii* (Herpin, 1925) and *Ostrea virginea* (Galtsoff, 1940), but they are comparatively few in number. Whether or not the inducement subsequently became mutual, as noted by Coe (1947) for *Tivela stultorum*, was not evident, but the result was an 'epidemic' spawning such as that described by Hargitt (1910) for *Hydroides dianthus*, and those quoted by Thorson (1950) for other polychaetes and certain molluscs. The chances of all the eggs spawned being fertilized were thus greatly increased because they were present simultaneously with enormous quantities of sperm in a comparatively small volume of water. Unfertilized eggs were very scarce at the onset of the flood, so that the mode of spawning was seemingly an extremely efficient one.

Laboratory Observations on *Saccoglossus horsti*

Over the past 4 years some 200 mature specimens of *S. horsti*, along with a considerable quantity of their native mud and sand, were transported to Bangor and maintained in a healthy condition for periods of varying duration up to 6 months. This material was required for embryological purposes, so that observations on spawning were incidental. Nanoplankton cultures were provided as food. The aquaria were aerated.

After an acclimatization period of 1 or 2 days, the specimens settled down in burrows which they frequently made along the glass sides of the aquaria. Observation of their behaviour was thus greatly facilitated.

The surface of the mud, particularly in the immediate vicinity of burrows known to be occupied by females, and the interiors of any burrows alongside the walls of the aquaria, were carefully scrutinized at regular intervals daily, for the first 6 weeks after the collection and at less frequent intervals afterwards. Since the aquaria were situated in reduced light, well away from any

sunshine, eggs were difficult to see against the mud and silt which invariably settled in the aquaria. Some illumination was essential, and a small spot-light electric torch proved extremely useful. The beam from this could be directed in through the sides of the aquaria, and along the surface of the mud. Egg clusters illuminated in this way could be seen clearly against the dark substrate. It was also useful for the examination of the remoter regions of the burrows.

Although the author was never fortunate enough to observe any spawning within the 'open' burrows along the walls of the aquaria, several instances of spawn issuing from the burrows were recorded. Although these were in the main exactly as observed in the field, occasions were noted when fertilized and unfertilized eggs were seen to be exuding from the burrows. They flowed out in a manner which suggested that the female was pushing them, for her proboscis appeared at the mouth of the burrow from time to time, as more and more eggs were forced out on to the surface. The tip of the proboscis was observed once, under similar circumstances, in the field.

The enveloping mucus of the egg masses seemed to dissociate more rapidly in the aquaria. Several times eggs were found lying loose on the surface, with no evidence of any mucus around them. Some 50% of these were fertilized when discovered. This suggested that the dissociation of the mucus was not due to the action of the sperm alone, but to other factors, possibly the pH of the surrounding medium.

Sperm clouds observed in the laboratory were dispersed by the aeration currents and were similar to those seen in the field. Microscopic examination of a sample taken from one of these clouds showed that the sperms were solitary, and very active. Isolated samples of naturally and artificially released sperms maintained their vigour for several hours. One sample accidentally raised to 29° C. still contained numerous active sperms.

Fertilizations were carried out with naturally spawned eggs, and artificially as well as naturally released sperms. Freshly spawned eggs did not erect their membranes, after the addition of sperms, as rapidly as those which had been spawned for some time. At 16–17° C. a maturation period of 30 min. to 1 hr. ensued before impregnation could be effected. The eggs remained fertilizable for periods varying from 6 to 10 hr. Mature eggs, released some 2–3 hr. prior to the addition of sperms, erected their fertilization membranes within 10–15 min. On one occasion a few drops of a sperm suspension were injected into the burrows of several ripe females, and small clusters of eggs were observed around the mouths of many of these burrows the following morning, some 10 hr. later. No further experiments of this nature were carried out, but this single observation suggested that the females were induced to spawn by the presence of sperm.

Breeding Season of *Saccoglossus horsti* and *Saccoglossus cambrensis*

Collections were made in the Solent area during the periods 14. vi. 46–16. vi. 46; 20. v. 47–23. v. 47; 7. v. 48–12. v. 48 and 11. v. 49–16. v. 49. Some 400 specimens were examined in all. Collections could not be made earlier than May, but from the general condition of the gonads, and the paucity of spent or partially spent specimens, it was concluded that the first three collections had been made prior to the main spawning crisis for those years, and during the first main crisis for the latter. This conclusion is borne out by subsequent records of spawning in the aquaria, for apart from those stimulated to spawn by the 'shock' of collection, the majority spawned during the following 4–6 weeks. Whilst recognizing that the artificial conditions under which the animals were maintained may influence their behaviour, it is felt that the records of spawning, thus obtained, give some indication of the duration of the breeding season and the conditions under which it probably takes place.

Spawning was first recorded in the laboratory by Dr E. W. Knight Jones on 20. v. 46, and subsequently by the author from 17. vi. 46 to 15. vii. 46; 25. iv. 47 to 30. v. 47; 18. v. 48 to 1. vi. 48, and on three occasions 15. v. 49, 1. vi. 50 and 2 .vi. 50 in the field. These records were mainly of one, often two, rarely three specimens spawning in any one day. There was never any indication of a concerted effort comparable to the field records.

Temperature records show that specimens will spawn over a fairly wide range, from 13·5 to 21·0° C. A temperature rise prolonged over 2 or 3 days invariably resulted in some specimens spawning. Some 60% of the records were made at 16–17° C., 30% below, and the remainder above. Many eggs were spawned at comparatively low temperatures (14·5° C.) and failed to develop beyond the 3rd or 4th cleavage. Others spawned at higher temperatures (20° C.) suffered the same fate, but those produced between 16 and 17° C. developed normally and the larvae were successfully reared until they had several pairs of gill-apertures.

The occurrence of several spent specimens amongst those examined from the Solent collections of June 1946 indicated that some spawning had already taken place, probably during the previous spring tides. Air and sea temperatures in the area for this period were suitable, and rose from 11·1 to 15·6° C. during the period 27. v. 46–30. v. 46, whilst the main Southampton water was *c.* 14·4° C. Inshore temperatures would have been proportionately higher, particularly in the sheltered regions, and thus ideal for spawning.

In the collections of May 1947 a fairly high proportion of immature specimens was noted, and the impression gained was that spawning had not yet commenced for that season, but it did so in the laboratory some 4–5 days later.

Specimens collected during May 1948 were extremely ripe, and very difficult to handle without causing injury. Several hot days followed their

transfer to the laboratory, and spawning commenced on the 18th, a week after they had been collected. The extreme ripeness of the numerous specimens observed in the field indicated the imminence of a spawning crisis, possibly the first of the season, for spent specimens were very rare. Air temperatures for the period 7. v. 48–11. v. 48 rose from 11·1 to 15·6° C., the sea temperature rising from 12·2 to 14·4° C., but the air temperature dropped to 13·3 °C. the next day, and subsequently to 10° C. for the 13th and most of the 14th. This might well have delayed the spawning until the next temperature rise took place during the afternoon of the 14th, when it rose to 16·7° C., and then to 20° C. on the 15th. Temperatures remained at about this level throughout the next few days, but since the tides had lapsed into neaps during this period it is thought that the full effect of the rise would not be felt, and that in all probability spawning did not start until the onset of the next series of spring tides when there were several warm days and maximum air temperatures varied from 19 to 22° C.

At the time of the mass spawning in the Solent (15. v. 49) the temperature of the shallow surface water in the inlet during the ebb was 17·5° C., and that of the sand varied from 15 to 16° C. according to the degree of exposure to the sun. The temperature at a depth of 6 in. in the sand was some 2° C. below that recorded at the surface. The sea temperature[1] was at 12·8° C. on that day, having risen steadily from 11·6° C. recorded on 8. v. 49, whilst the air temperature had risen with slight fluctuations from 7·8° C. at 18.00 hr. on 11. v. 49 to 14·4° C. at 12.00 hr. and to 16·7° C. at 18.00 hr. on 15. v. 49. The phenomenon was repeated on two successive occasions during the spring tides of June, 1950. The beds had been examined during the ebb tides of the previous four days, but it was not until the afternoon ebb of 1st June that spawning commenced. In every respect the progress of events was comparable to those observed in 1949. Spawning began some 30 min. after the tide had receded, and was mainly confined to those areas of the beds which were covered by shallow pools. The temperature of the water in these pools was 21° C., and that of the underlying sand was 17° C. at a depth of 6 in. below the surface. Although several egg masses were observed within a few minutes of the discovery of the first it was some time before the first sperm cloud was seen. The intensity of spawning was greater than that experienced previously, and an arbitrarily chosen square metre of the shore contained 125 casts, 21 egg masses and 5 sperm clouds. The production of egg masses reached its climax some $1\frac{1}{2}$–2 hrs. after the tide had ebbed, whilst the production of sperm clouds continued vigorously until the flood had commenced, when it abated markedly. Examination of the area at 6 a.m. the following morning failed to reveal any traces of the spawning. The water in the surface pools at this hour had fallen to 17·2° C., but that of the sand remained at 17·0° C. During the afternoon

[1] The sea temperatures quoted are for the main Southampton Water, unless otherwise stated.

ebb of this day the water temperature rose to 21·5° C. and that of the sand to 17·5° C., and spawning commenced as on the previous day.

Since similar weather and tidal conditions prevailed for the succeeding two days it is likely that the intermittent spawning would continue until the tides lapsed into neaps. A temperature rise seems to have played a major part in initiating the mass spawning observed on these three occasions, for they all occurred after the shore had been subjected to hours of fairly intense sunshine over a period of several days. Orton (1920) and Thorson (1946, 1950) have shown that temperature influences the spawning of numerous marine invertebrates. Korringa (1947) cites several examples where tidal influences also play an important part. It would seem that both factors are probably concerned in the spawning of *S. horsti*.

Specimens of *S. cambrensis* have been examined at all times of the year, and whereas they were apparently always ripe, there was very little evidence of any spawning. A close inspection of the more densely populated areas in the Menai Straits made during the spring tides of June and July 1949, yielded several empty egg cases. These were discovered in the sand around the mouths of burrows. They were very similar to those of *S. horsti*, but in the absence of any embryos the identification must remain uncertain. One egg contained a cream-coloured ovoid embryo which was densely ciliated, and very like the late gastrula stage of *S. horsti*. It rapidly disintegrated in the laboratory, so that little else can be said about it. Tow-nettings with a no. 15 bolting silk net were made over the surface of the sand just prior to its exposure by the receding tide. These yielded several more empty egg cases, all of the same size and appearance. Since these were discovered within a short period of the mass spawning in the Solent, and under comparable weather conditions, it is possible that a spawning had already taken place in the Menai Straits and that the egg cases were the remnants of eggs which had hatched either in the burrows and were subsequently expelled, or in amongst the sand grains on the surface. Some fifty specimens of a *Saccoglossus* species (Burdon-Jones, 1950*b*) examined in the Sound of Mull, during the spring tides of August 1948, revealed that ripe females and, to a lesser degree, ripe males, were comparatively rare. Numerous specimens were difficult to sex because they were either spent, or immature. The impression gained was that the main spawning, for that year, had already taken place. Numerous adult specimens of a species of *Protoglossus* (Burdon-Jones, 1950*a*) were examined during August, September and October 1949, and although mature specimens of both sexes were collected, they were very much in the minority, the paucity being most pronounced amongst the females. These observations, once more, suggest a breeding season at some time during the preceding few months, viz. May to July.

It would seem that the main spawning season for the British species of the Harrimanidae is mainly during the months of May to July. Mass spawning comparable to that described for *Saccoglossus horsti* is likely to be common to them all and to take place under similar climatic and tidal conditions.

Discussion

In the light of this new information, it remains for us to examine what is known of the spawning behaviour in the other species of Enteropneusta.

Bateson (1884) suggested that in *Saccoglossus kowalevskyi* the eggs and sperms, the latter aggregated in lobate masses, were released by a rupturing of the body wall. Spengel (1893) pointed out the improbability of this, basing his arguments on the mode of maturation of the gonads. His comments were borne out by the discovery of large genital apertures in mature *Glossobalanus ruficollis*, which Willey (1899) noted would enable eggs to be released without any difficulty. There was no evidence of rupturing in *Saccoglossus horsti*, or any evidence of increased mortality amongst spawning specimens in the laboratory or in the field. Rupturing and spermatophoric masses have been observed only in one other species, viz. *S. otagoensis* (Kirk, 1937, 1938), but this is a rock-pool inhabitant, and has a specialized mode of spawning in keeping with its habitat.

For *S. pusillus* Ritter & Davis (1904) recorded mature specimens in August, and suggested that the breeding season extended over at least 4 months. Davis (1908) discovered that the main breeding season was in January and February. The genital products were released through the genital apertures as in *S. horsti*, but the eggs were discovered closely packed and somewhat flattened, and adhering to the walls of inhabited burrows. Their appearance and situation suggests that they were not expelled with the main clutch, but had been pressed into the mucus lining of the burrow whilst spawning was taking place. In this position they could be fertilized by sperms carried into the burrow by the aerating currents of the animal within it, and thus aerated and protected they would develop. In the light of the observations on *S. horsti* however, these eggs might be regarded as a remnant of the main egg mass which had been expelled from the burrow and probably washed away by the tide, or camouflaged by silting. Since the habitat was a muddy one, this could easily have occurred and, in consequence, the eggs might well have been overlooked.

Stiasny (1913) made comparable observations on *Balanoglossus clavigerus*. It is significant that he noticed eggs were easily overlooked within the burrows because their colour closely resembled that of the sand. Under such circumstances it is probable that they might also be overlooked if lying on the surface.

On this interpretation, spawning of *Saccoglossus pusillus* may be comparable to that noted in *S. horsti*, and so also might that of *Balanoglossus clavigerus*, for Heider (1909) recording observations made on specimens in the laboratory noted:

> Am 12. Juni, um 6 Uhr nachmittags fand sich an der Mündung einer solchen Wohnröhre ein schleimiger Laichklumpen von etwa Nussgrösse. Der Schleim, in welchem Hunderte von Eiern eingeschlossen waren, ist ungemein zerfliesslich, und nachdem der Laich herauspipettiert war und das Gefäss in welchem er sich nun befand, einigem Schütteln ausgesetzt war, löste er sich scheinbar vollständig auf.

Because the observations were made on specimens in an aquarium, van der Horst (1927–39) queried the probability of such egg masses occurring in the field. Nevertheless, they occurred in *Saccoglossus horsti*, both in the laboratory and on the shore, so that we must regard Heider's observations as being indicative of a similar occurrence in *Balanoglossus clavigerus*, although this was never confirmed by Stiasny.

Kowalevsky (1866) made the supposition that, 'Es ist wahrscheinlich, dass der *Balanoglossus* Eierschnüre legt, in der Art, wie es die meisten Nemertinen und viele Anneliden thun', but Agassiz (1872) failed to find any whilst working on *Saccoglossus kowalevskyi*. Subsequently, this theory was strongly deprecated by Spengel (1893) on the grounds that the gross morphology of the gonads would make it impossible. The observations on *S. horsti* tend to invalidate this statement, for when first expelled from the burrow the eggs of this species are in a cord which coils on itself and rapidly fuses into a single mass. The existence of such cords is not necessarily universal, but they have also been described in *Glossobalanus minutus* (Dawydoff, 1928). The persistence of the cord undoubtedly depends on the conditions under which it is expelled from the burrow. Certain specific variations might well occur.

From the above observations and those of Russell (1925) and others, on the seasonal occurrence of enteropneust larvae in the English Channel, North Sea and various parts of the world, and the large numbers of Tornaria larvae of the same size that are often found together, it might be concluded that an 'epidemic' spawning comparable to that described for *Saccoglossus horsti*, and initiated and perpetuated in a similar manner, is common to all the littoral and possibly some sub-littoral species of the families Ptychoderidae and Harrimanidae.

Summary

The genital products of *Saccoglossus horsti* are discharged within the burrows and expelled after the tide has ebbed. They are not retained in the burrows for any length of time.

Fertilization occurs mainly in the overlying surface water, or during the flood.

An 'epidemic' spawning was observed on three occasions in the field.

A rise of temperature to about 16° C. is regarded as the essential factor primarily responsible for initiating the spawning.

The females were observed to spawn before the males. Some reciprocal inducement might have occurred.

The breeding season in the Solent area is mainly confined to the months of May, June and July, and is seemingly dependent on climatic and tidal conditions during these months.

The spawning behaviour of other species of the Enteropneusta is discussed.

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THE IDENTIFICATION OF BRITISH SPECIES OF THE GENUS *ENSIS* SCHUMACHER (LAMELLIBRANCHIATA)

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(Plate I and Text-figs. 1–5)

Introduction

Winckworth (1932) lists three British species in the genus *Ensis* Schumacher. Two of these, *E. ensis* (L.) and *E. siliqua* (L.), are recorded by Linnaeus in the genus *Solen*; the third, *E. arcuatus* (Jeffreys), was considered by Jeffreys (1863) to be a variety of *E. siliqua*. Winckworth has, however, raised it to specific rank, without giving any reasons. In the present paper Winckworth's classification is followed, a note on the validity of the species appearing at the end.

Examination of specimens in various collections has revealed the confusion that has arisen in the identification of the species of *Ensis*: consequently many records are unreliable. Identification has proved difficult partly on account of a dearth of good illustrations of the three species, and also through the lack of any diagnostic distinguishing characters. Although *E. siliqua* is illustrated in many works, there are few good drawings of *E. ensis*, and some (Sowerby, 1887, for example) have illustrated *E. arcuatus* as *E. ensis*. Forbes & Hanley (1853) have an engraving of *Solen ensis* var. *magna* (=*E. arcuatus*), but failed to illustrate *Ensis ensis*.

I am indebted to the following for assistance in obtaining specimens, and for other information: Miss D. Atkins, Messrs H. J. Baal, J. H. Barrett (Warden, Dale Fort Field Centre), H. H. Bloomer, T. E. F. Carr, P. G. Corbin, Major A. A. Dorrien-Smith, Messrs G. R. Forster, N. S. Jones, The Director of the Millport Marine Station, Dr W. J. Rees, Messrs D. P. Sharman, A. G. Southward, G. M. Spooner, J. Thompson, C. C. Wilton-Davies, and the late R. Winckworth.

I am grateful to the Linnean Society of London for allowing me to examine type specimens; and to Dr R. Tucker Abbott, Division of Mollusks, U.S. National Museum, for kindly supplying photographs of Jeffreys' original specimens of *E. arcuatus*.

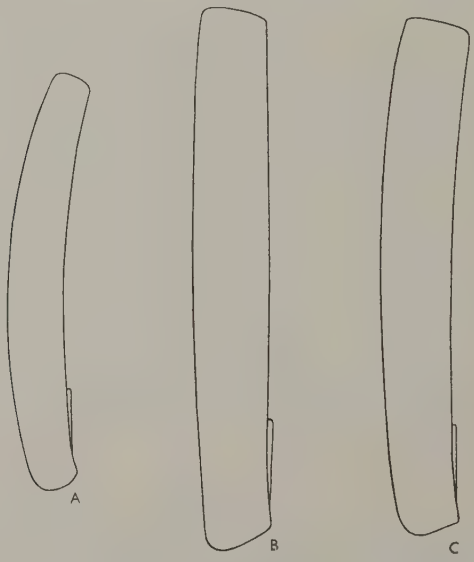
The Genus *Ensis*

The genus *Ensis* comprises lamellibranchs with elongate equivalve shells, gaping at either end. The anterior end of the shell is not constricted, and the

hinge is terminal, having two teeth in the left valve, between which fits the single tooth of the right valve. There is a long external ligament. The two siphons are short and are surrounded by cirri. A fourth pallial aperture is present.

Distinguishing Characters

In several of the distinguishing characters to be described there is some overlap owing to variation among individuals of a species. Consequently it is often necessary to employ all the available characters before a 'difficult' specimen can be identified.



Text-fig. 1. Outline of *Ensis* shells, × 3/5. A, *E. ensis*; B, *E. siliqua*; C, *E. arcuatus*.

The Shell

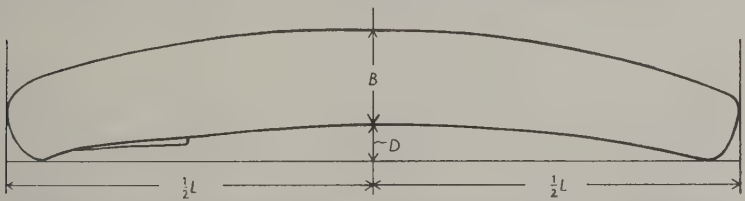
This remains the primary means of identification, both of the genus and species. The shell of *Ensis* is elongated along its anterior-posterior axis. Hence the pedal end is morphologically anterior, and the siphonal end is posterior. The long edge bearing the hinge is dorsal.

Length. The length attained by adult specimens differs in the three species. *E. siliqua* reaches a maximum of 20 cm., while *E. arcuatus* and *E. ensis* attain 15 and 10 cm. respectively. In many populations, however, these lengths are not reached, and Text-fig. 3 gives some indication of the lengths usually encountered.

Length/breadth ratio. Measurements of shell breadth are made as shown in Text-fig. 2. Results obtained from measurements of about 100 specimens from different localities are shown in Text-fig. 3, and summarized in Table I. The mean ratio is 6·80 in *E. siliqua*, 7·18 in *E. arcuatus*, and 7·80 in *E. ensis*. The range in proportions within each species is such, however, that there is some overlap between the species. In *E. siliqua* the shell tends to broaden in larger sizes, in *E. arcuatus* it remains fairly constant, whereas in *E. ensis* there is a tendency for it to become narrower.

Ford (1925) found a difference in the proportions of very small specimens of *E. ensis* and *E. arcuatus*. (He does not state, however, at what point the shell breadth was measured.) In *E. arcuatus* ranging from 7·5 to 21·0 mm. in length the mean ratio was 5·08, and in *E. ensis* ranging from 5·0 to 22·5 mm. the mean ratio was 6·44. Here again there was some overlap between the two species.

Thus the length/breadth ratio is not a reliable distinguishing character where only a few specimens from a population are available.



Text-fig. 2. Method of measuring breadth (*B*) and curvature (*D*) of an *Ensis* shell.

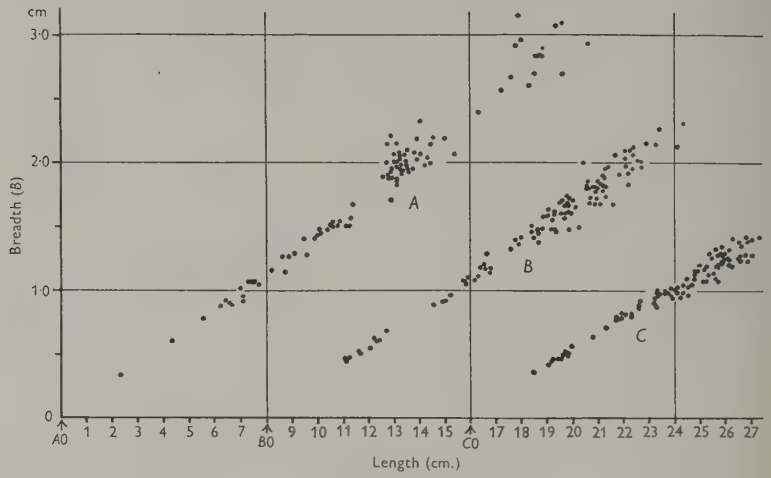
Curvature. The most obvious difference between the species is in the shell curvature. A measure of the curvature of the dorsal edge of the shell is obtained as shown in Text-fig. 2. The dorsal edge of a single valve is placed against a straight edge on a special measuring board, so that the two ends touch the edge. The ligament is cut away as necessary to allow this. In *E. siliqua* the shell usually touches at the anterior end and at a point just behind the mid-region, as the shell is often slightly convex on the dorsal surface. The distance $B+D$ is measured by a vernier calliper, as is the breadth (B). 'D' is then obtained by subtraction.

In *E. siliqua* most specimens are straight or slightly convex, (Text-fig. 4) giving a 'D' of zero. 'D' is not more than 0·1 cm. in normal specimens. Two very small specimens show some degree of curvature; this results in a slight curvature in the hinge region in adult specimens.

In *E. arcuatus* curvature is variable, some being as straight as slightly curved specimens of *E. siliqua*.

In *E. ensis* curvature is greater than in *E. arcuatus*, the plots of the two species scarcely overlapping.

It will be noticed that 'D' becomes proportionately greater in large specimens. This is to be expected if the shells are growing in a curve approximating

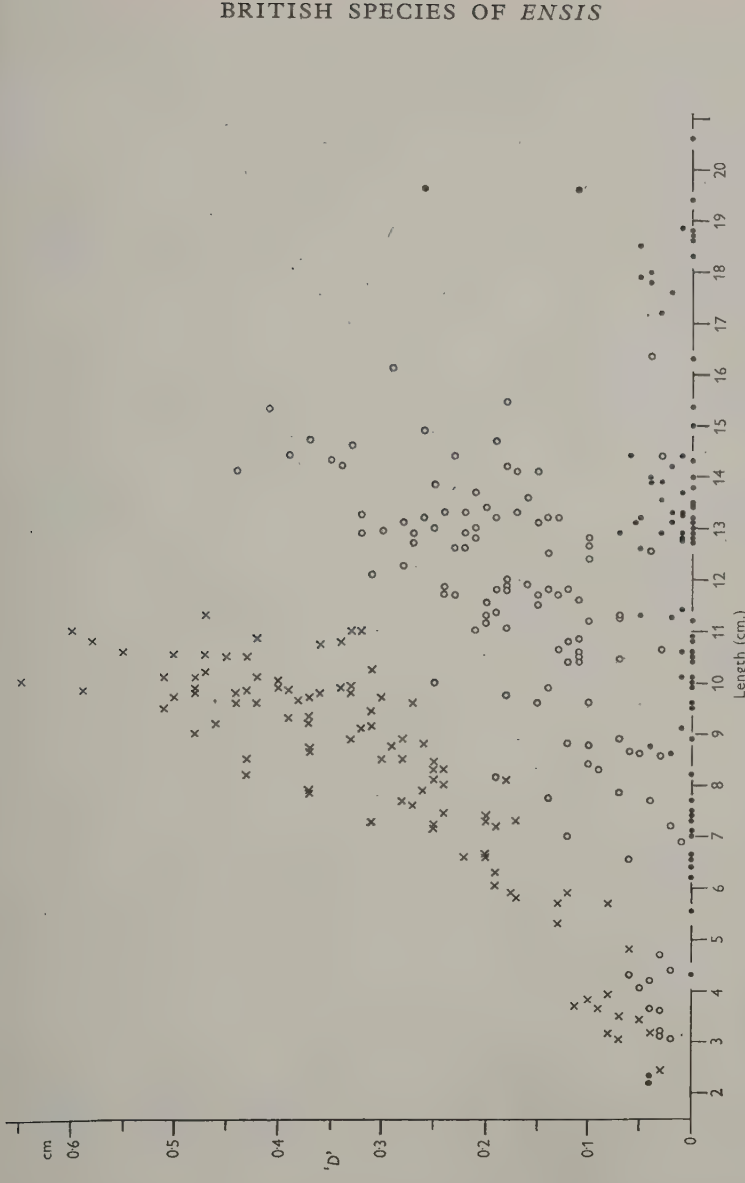


Text-fig. 3. Length-breadth relations of shells of *Ensis*: *A*, *E. siliqua*, 95 specimens from Broadsands, Torbay (6); Dale Roads, Milford Haven (6); Helford river, Cornwall (3); Millport (9); Paignton (59); Polesands, Exmouth (7); Salcombe (5). *B*, *E. arcuatus*, 112 specimens from Derbyhaven, Isle of Man (4); Eddystone shell-gravel (1); Grouville Bay, Jersey (10); Mewstone shell-gravel, Plymouth (1); Millport (3); Newton Haven, Northumberland (2); Salcombe, (52); Tresco, Scilly Is. (16); Yealm river (23). *C*, *E. ensis*, 101 specimens from Broadsands, Torbay (6); washed up on Dawlish Warren Beach (44); Grouville Bay, Jersey (5); St Aubin's Bay, Jersey (26); Salcombe (20). All shells are from material collected alive, except for some of those from Dawlish Warren Beach.

Note that the plots of *A*, *B* and *C* have different origins (indicated by arrows).

TABLE I

	Shell length (cm.)	Number examined	Length/breadth ratio		
			Mean	Maximum	Minimum
E. siliqua	0 – 4·0	1	7·06	—	—
	4·1– 8·0	13	7·09	7·72	6·28
	8·1–12·0	21	7·06	7·54	6·74
	12·1–16·0	44	6·67	7·50	5·84
	> 16·0	16	6·55	7·26	5·66
	All sizes	95	6·80	7·72	5·66
E. arcuatus	0 – 4·0	6	6·92	7·16	6·49
	4·1– 8·0	12	7·23	7·61	6·65
	8·1–12·0	46	7·20	8·29	6·71
	12·1–16·0	46	7·17	8·17	6·20
	> 16·0	2	7·32	7·56	7·08
	All sizes	112	7·18	8·29	6·20
E. ensis	0 – 4·0	11	7·20	7·64	6·83
	4·1– 8·0	28	7·66	8·39	7·20
	8·1–12·0	62	8·01	9·07	7·25
	All sizes	101	7·80	9·07	6·83



Text-fig. 4. Measurements of shell curvature ('*D*', Text-fig. 2) against shell length. The shells are those used for breadth measurements in Text-fig. 3. ×, *E. ensis*; ○, *E. arcuatus*; ●, *E. siliqua*.

to an arc of a circle. The points would then form part of an ellipse, the proportions of which would naturally vary according to the scale adopted for the two axes of the graph.

Taper. In *E. siliqua* the dorsal and ventral edges are almost parallel, with little taper at either end (Text-fig. 1 and Pl. I, fig. 1). In *E. arcuatus* there is some slight taper at the posterior end. In *E. ensis*, however, the ventral edge approaches the dorsal in the posterior third of the shell, producing a most pronounced taper. Although no measurements of taper have been made it would appear that the degree of taper in extreme specimens of *E. arcuatus* is similar to that of a typical *E. ensis*, and vice versa.

Shape of the ends. The posterior end of the shell in all three species is truncated, that of *E. ensis* being if anything a little more rounded than in the other two. The anterior ends of *E. siliqua* and *E. arcuatus* are similarly truncated, but that of *E. ensis* is rounded, as shown in Text-fig. 1.

Colour. The outside of the shell is divided diagonally into two areas of a different colour. The dorsal area is white or liver-coloured, while the ventral area varies from pale yellow to chestnut brown in colour. *E. ensis* is usually lighter in colour than the other species, but all shades from yellow to dark brown may be found in different populations of all three species. Small individuals are lighter in colour than adults from the same locality, and are often spotted with dark brown (Pl. I, fig. 2). The spots disappear or become indistinct in adults.

Soft Parts

Bloomer (1901–2) has studied the anatomy of *E. ensis* and *E. siliqua*. He found only minor differences between them, of little value in identification. Mr Bloomer informs me that his specimens were obtained from the Specimen Department at Plymouth. Since *E. ensis* is rare at Plymouth, most of the records in the *Plymouth Marine Fauna* (Marine Biological Association, 1931) being incorrect identifications of *E. arcuatus*, it seems possible that Bloomer was in fact comparing *E. arcuatus*, not *E. ensis*, with *E. siliqua*.

The internal anatomy of *Ensis* has not been examined in any great detail. The gross anatomy of all three species is very similar. Sections of the gills failed to show any significant differences in structure. Two characters have, however, been found useful for identification.

Colour of the foot. A difference in the colour of the foot has been noted by several authors. In *E. siliqua* and *E. arcuatus* it is creamy white in colour, reticulated with fine brown lines. The colour varies with the degree of distension or contraction of the foot. In *E. ensis* the foot is a pale reddish brown, and is also reticulated. The difference in colour is not great, but is useful in sorting out a mixed population of *E. ensis* and *E. arcuatus*.

The fourth aperture. In the posterior half of the body the mantle edges are fused ventrally, but anteriorly fusion is very weak, so that the mantle folds may be readily separated back as far as a small opening, the fourth aperture

(Text-fig. 5,A). The weak fusion is brought about by a cuticular junction of the mantle edges (Atkins, 1937).

Yonge (1948) believes the aperture to be a 'safety valve which permits the ventral extrusion of some of the water in the mantle cavity when these rapidly burrowing animals make the sudden muscular contractions involved in downward movement'.

The aperture is bordered by a row or rows of papillae, which interdigitate when the shell is closed. The papillae occur in about equal numbers on each side of the aperture. There is considerable variation in the number of papillae in each species, but *E. siliqua* tends to have more than the other two:

E. siliqua. Thirty-four specimens from Paignton, Devon. Number of papillae on one side of the opening: mean, 20·9; maximum, 40; minimum, 9.

E. arcuatus. Forty-two specimens from Tresco, Scilly Isles. Mean, 10·5; maximum, 26; minimum, 5.

E. ensis. Twelve specimens from St Aubin's Bay, Jersey. Mean, 12·0; maximum, 15; minimum, 8.

The species differ more in the form than in the number of papillae. In *E. siliqua* the papillae occur in more than one row, in a staggered arrangement. In small specimens they are simple (Text-fig. 5,G) but in those over about 7 cm. in length they are branched, or compound (Text-fig. 5,B, E and F). In side view they often resemble molar teeth. The form of the papillae can be distinguished with a lens in living specimens. Those illustrated in Text-fig. 5 are preserved in alcohol; the papillae do not seem to contract to any great extent in preserved specimens.

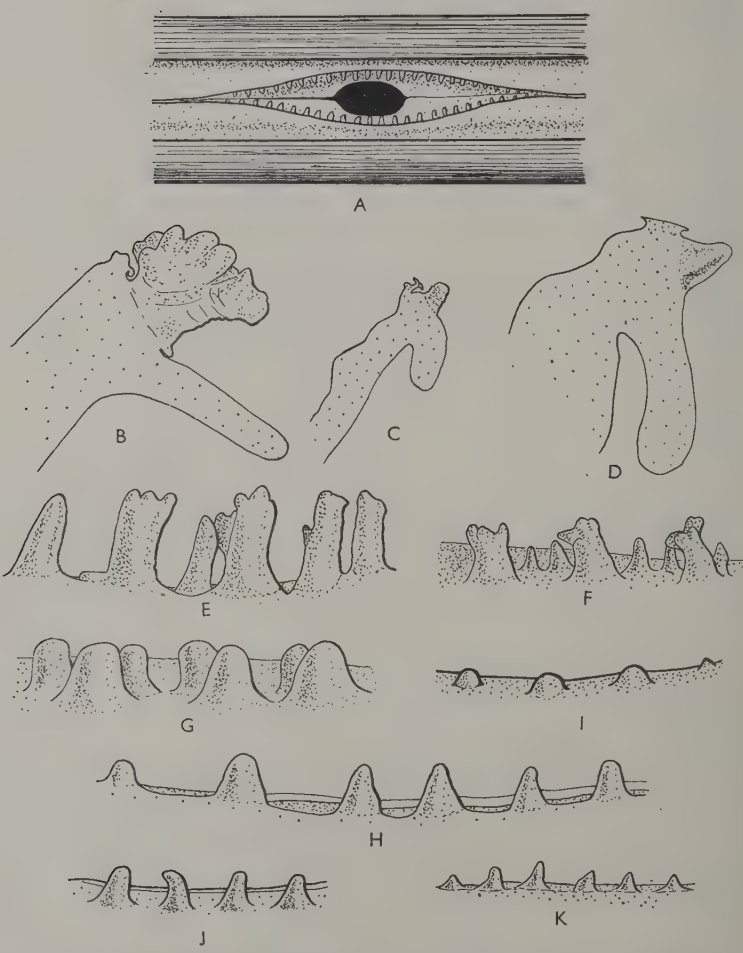
In *E. arcuatus* the papillae are simple, and in a single row (Text-fig. 5,H, I). Rarely, in large specimens, they may become bifid or club-shaped, but never assume the compound form typical of *E. siliqua*.

In *E. ensis* the papillae are similar to those of *E. arcuatus* (Text-fig. 5,J, K).

The form of the papillae of the fourth aperture is the only certain method of distinguishing adult specimens of *E. siliqua* and *E. arcuatus*. Certain separation is more difficult where specimens are still too small to show differences in these papillae, but the curvature of the shell is often some guide.

Validity of the Species

Constant morphological differences have been found between the three species of *Ensis*. These differences are slight however, and might be attributable to the effect of environment on a single species. *E. siliqua* occurs in clean sand at L.W.S.T., extending a little below extreme low-water mark. *E. arcuatus* lives in coarse sand or fine gravel at L.W.S.T., and extends out into deeper water. *E. ensis* inhabits bottoms of fine, sometimes slightly muddy, sand; rarely occurring on the shore. Thus the three species are not often found living together.



Text-fig. 5. Morphology of the fourth aperture. A, ventral view of the aperture in *E. siliqua*, × 4. The shell is shown slightly gaping to reveal the mantle folds surrounding the opening. The anterior end is to the left. B–D, thick sections through the edge of the mantle opposite the aperture, the latter being on the right of the lip (lower right). A papilla (compound in *E. siliqua*) is shown top right. B, *E. siliqua*; C, *E. ensis*; D, *E. arcuatus*. All are × 19·5. E–K, papillae viewed from inside the aperture, looking outwards: E, *E. siliqua*, length 15·0 cm., × 19·5; F, *E. siliqua*, length 13·7 cm., × 19·5; G, *E. siliqua*, length 7·0 cm., × 59; H, *E. arcuatus*, length 14·75 cm., × 19·5 (all papillae on one side shown); I, *E. arcuatus*, length 7·9 cm., × 19·5; J, *E. ensis*, length 10·05 cm., × 19·5; K, *E. ensis*, length 4·52 cm., × 19·5.

Fig. 1. Shells of adult *Ensis*. ×0·47. Left to right: *E. siliqua*, *E. arcuatus*, *E. ensis*.

Fig. 2. Small individuals of *Ensis*. ×2·4. Left: four specimens of *E. ensis* dredged in Whitsand Bay. Right: two specimens of *E. arcuatus* from the same locality. The foot may be seen projecting beyond the end of the shell in some of the specimens.

Occasionally, however, mixed populations have been found living in the same grade of soil in one locality. The following instances have been recorded:

E. siliqua living with *E. ensis*: Broadsands, Torbay, in fine sand.

E. siliqua living with *E. arcuatus*: south side of Millbay, Salcombe, in fine sand; Jeffreys (1863) records both species from Belgrave Bay, Jersey.

E. arcuatus living with *E. ensis*: in sand in St Aubin's Bay and Grouville Bay, Jersey, in Whitsand Bay, and in coarse muddy sand at Millbay, Salcombe.

Since the three forms maintain their distinctive characters when living together, it seems probable that they are separate species.

Summary

The diagnostic characters of the British species of *Ensis* are described. The shell remains the primary means of identification, but additional characters in the soft parts are necessary for certain recognition. The three forms of *Ensis* described are considered to be valid species.

Table II. Summary of Distinguishing Characters

	E. siliqua	*E. arcuatus*	*E. ensis*
Length of shell	20 cm.	15 cm.	10 cm.
Shell curvature	Straight	Slightly curved	More curved than in *E. arcuatus*
Taper of posterior end	None	Slight	Marked taper
Anterior end	Truncated	Truncated	Rounded
Foot colour	Cream-white	Cream-white	Pale red-brown
4th aperture:			
Rows of papillae	Staggered	1 row	1 row
Shape of papillae	Compound	Simple	Simple

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A STATISTICAL STUDY OF VARIABILITY IN CATCH OBTAINED BY SHORT REPEATED TRAWLS TAKEN OVER AN INSHORE GROUND

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(Text-figs. 1–3)

Introduction

The numerous quantitative studies on various types of fishing gear have always been chiefly directed to the relation between the proportion of size-groups in the sample and in the population, and to the effect of mesh size on this relation. There have been only a small number of controlled experiments on the variability of replicate samples. While the former type of information is fundamental in fishery investigations, the latter, equally necessary, becomes an essential preliminary in a detailed ecological approach to fishery problems, for it is then necessary to know whether hauls taken at different times or in different places have given significantly different catches.

Thompson (1928) considered sampling problems in his extensive haddock investigations. Data are given from two series of hauls (using a 60 or 50 ft. otter trawl), each series extending over several days; and he points out that these samples (1 hr. trawling, *c.* 350 fish per catch) gave an adequate representation of the proportion of size-groups. Using logarithmic values of his catches (see below) the coefficients of variation were 27 and 51% for the two series.

Hickling (1933), using a full-sized trawl and working on hake, also gives data for repeated hauls taken under various conditions, although like Thompson he was more particularly concerned with the size-frequencies in his samples. The coefficient of variation for catches (log values) of hake varied from 25 to 88%, this range including results from R. V. *George Bligh* and from commercial trawlers.

Gardiner & Graham (1925) have considered the working error of Petersen's young fish trawl, and the design of these experiments was similar to that of the present work. They counted a number of species in ten replicate hauls and they give coefficients of variation calculated on actual numbers varying from 27% for *Euthemisto compressa* to 54% for *Aglantha digitalis*. The analysis of variance of their data (log values) using those animals occurring in all samples is given in Table I.

The mean square for hauls is significant when tested against $H \times S$ and the estimated log standard deviation for a single observation $\sqrt{s_H^2 + s_{HS}^2}$ is 0·1936, corresponding to a coefficient of variation of 56%.

TABLE I

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects			
Hauls (H)	9	0·9835	0·1093
Species (S)	6	28·2730	4·7120
Residual			
$H \times S$	54	1·3792	0·0255
Total	69	—	—

This present work consists of the analysis of the variability of a series of replicate hauls taken over a prescribed ground with the same gear and as far as possible under controlled conditions. In order that the results shall be of value to other workers it is necessary to describe both the gear and working conditions in some detail.

METHODS

The Gear and Method of Working

A standard type V.D. trawl, as described by Davis (1936, p. 104), was used, the detailed specifications being as follows: doors, 7 ft. 3 in. × 3 ft. 10½ in.; bridles, 20 fathoms; headline (fitted in part with Phillips's patent plane floats), 54 ft.; foot rope, 72 ft.; size of meshes, wings 5 in., square 5 in., belly 3½ in., cod-end 3 in.

The trawl was shot and hauled in the usual manner (Davis, 1936) from the M.V. *Calanus* under the supervision of Captain R. Souter.

The Ground and Working Conditions

The area trawled was an inshore ground on the east side of Bute, in the vicinity of Scoulag Point (full Kilometre National Grid Reference 26/1160–1159). A dan buoy was laid down and each haul was made on a somewhat elliptical course over the ground, starting and returning to the buoy. Positions were also checked by conspicuous objects on the shore. The bottom, which is here a sandy mud at 20 fathoms, shelves towards the centre of the channel. Tidal currents in this area are of the order of 1½ knots. During the trawling echo-soundings were taken, and are shown in Fig. 1, which indicates that each set of hauls was consistently taken over similar ground.

Three series of four replicate hauls were taken. Each haul lasted 30 min.; including shooting and hauling, each set of four hauls, all taken between 10.30 and 14.30 hr., occupied 3 hr. The weather conditions during all three series were moderate to good.

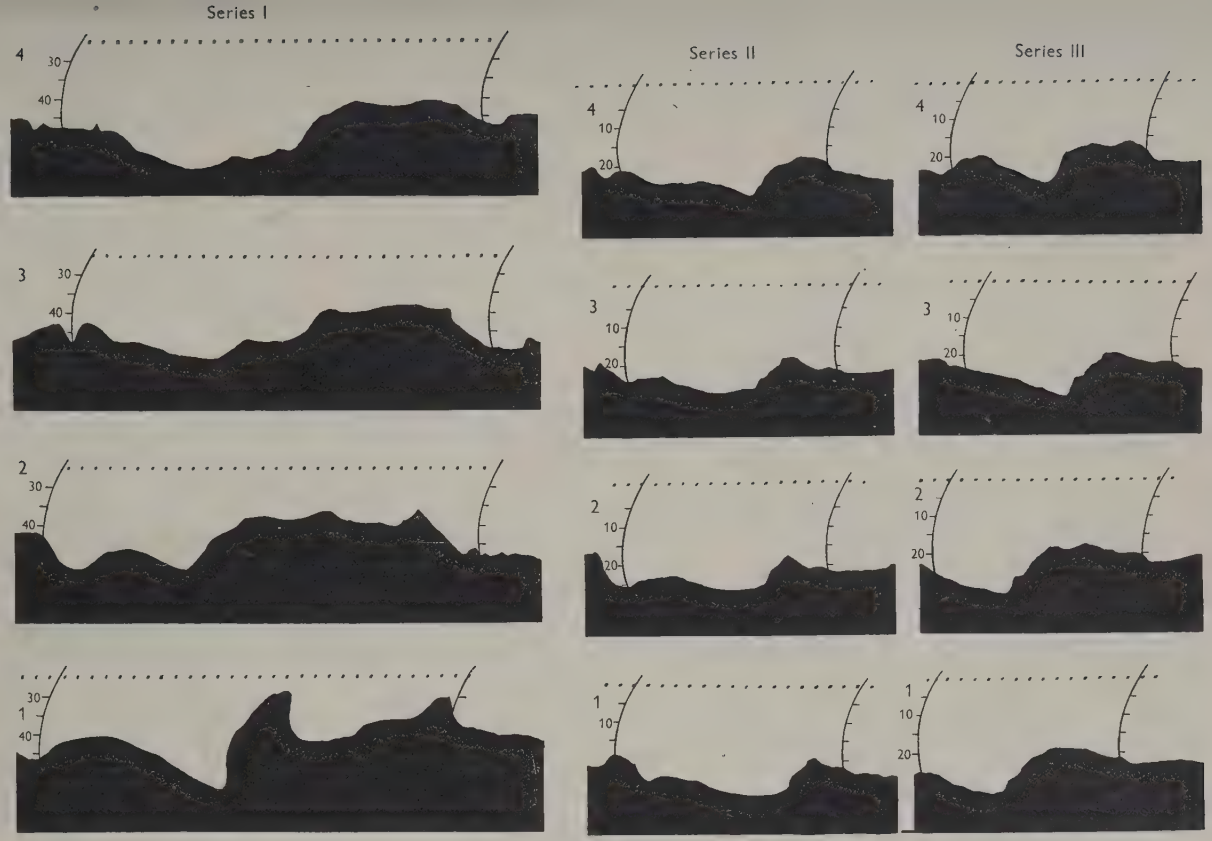

Fig. 1. Echo-soundings for hauls 1–4, series I–III. Series I time-marks at minute intervals; depth in metres. Series II (the echo-sounder was changed during the experiments) and III time-marks at 2 min. intervals; depth in fathoms. Marks at shooting and hauling.

The Collection of the Data

All the fish were measured in the standard manner, and a representative sample of each species taken for the examination of the stomach contents. The invertebrate fauna in each catch was also identified and counted. The major species were, the 'round' fish, *Acanthias vulgaris* Risso, *Gadus callarias* L., *G. merlangus* L., *G. minutus* O. Fr. Müller, *Merluccius merluccius* (L.); the 'flat' fish, *Pleuronectes platessa* L., *P. cynoglossus* (L.), *Drepanopsetta platessoïdes* (O. Fabricius); the crustacean *Nephrops norvegicus* L.

The Results

If the standard deviation of a series of catches is roughly proportional (as in plankton sampling) to the mean, a transformation from actual catches to logarithmic values should be made for the analysis of variance (Winsor & Clarke, 1940). A plot of standard deviation against mean catch for all species

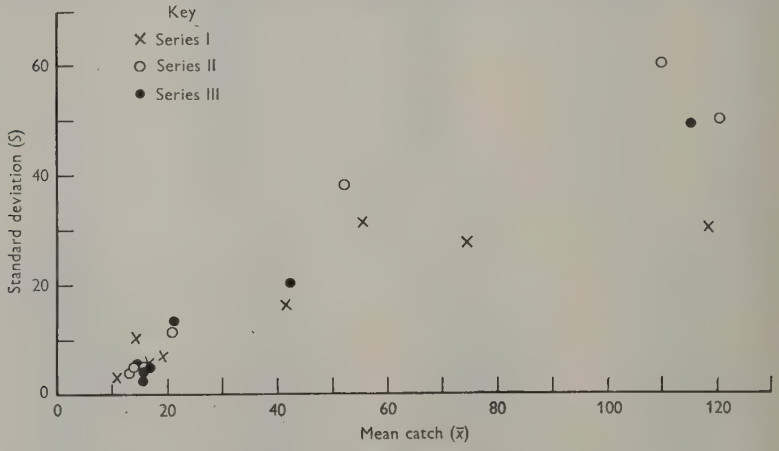

Fig. 2. Standard deviation (s) plotted against mean catch ($\bar{x}$) for each separate species from all the hauls of series I–III.

taken in all three series of hauls is given in Fig. 2. The two values are roughly proportional and the same trend is seen in the results of the earlier investigations referred to above. Logarithmic values of the catches will therefore be used in analysis.

As already pointed out, the work is primarily directed to a comparison of the numbers caught and their variability. However, the mean length for each species in the separate hauls and in the total catch are shown for all series in Table II and the percentage size frequency curves are given in Fig. 3, for some species present in moderate numbers. Since in some the number caught

TABLE II. THE MEAN LENGTH AND GRAND MEAN LENGTH (CM.) FOR SPECIES IN THE SEPARATE HAULS COMPRISING SERIES I–III

	Series I					Series II					Series III				
	Haul				Grand	Haul				Grand	Haul				Grand
Species	1	2	3	4	mean	1	2	3	4	mean	1	2	3	4	mean
Dogfish	—	—	—	—	—	61·8	60·4	61·9	59·2	60·8	—	—	—	—	—
Cod	40·0	36·5	45·7	48·9	43·8	45·0	47·6	47·7	51·5	48·0	49·9	48·7	45·4	35·8	45·0
Whiting	24·1	23·8	24·4	22·7	23·8	22·0	22·8	24·3	24·6	23·4	24·6	23·3	23·6	22·5	23·5
Poor Cod	18·3	16·3	14·2	16·0	16·2	15·3	19·0	19·0	17·8	17·8	—	—	—	—	—
Hake	37·6	36·2	39·1	27·8	35·2	—	—	—	—	—	39·0	35·9	35·1	37·1	36·8
Plaice	38·1	36·1	36·8	38·0	37·3	40·9	41·0	38·5	39·1	39·9	39·7	37·4	37·2	34·3	37·2
Witch	29·4	28·4	27·1	29·2	28·5	—	—	—	—	—	28·9	26·4	26·6	26·6	27·1
Long Rough Dab	20·0	20·2	20·2	19·4	20·0	18·1	18·9	20·0	19·9	19·2	19·0	20·5	20·2	20·9	20·2
Nephrops	16·5	15·5	14·2	14·1	15·1	14·0	14·1	14·0	14·2	14·1	15·0	14·9	15·5	15·7	15·3

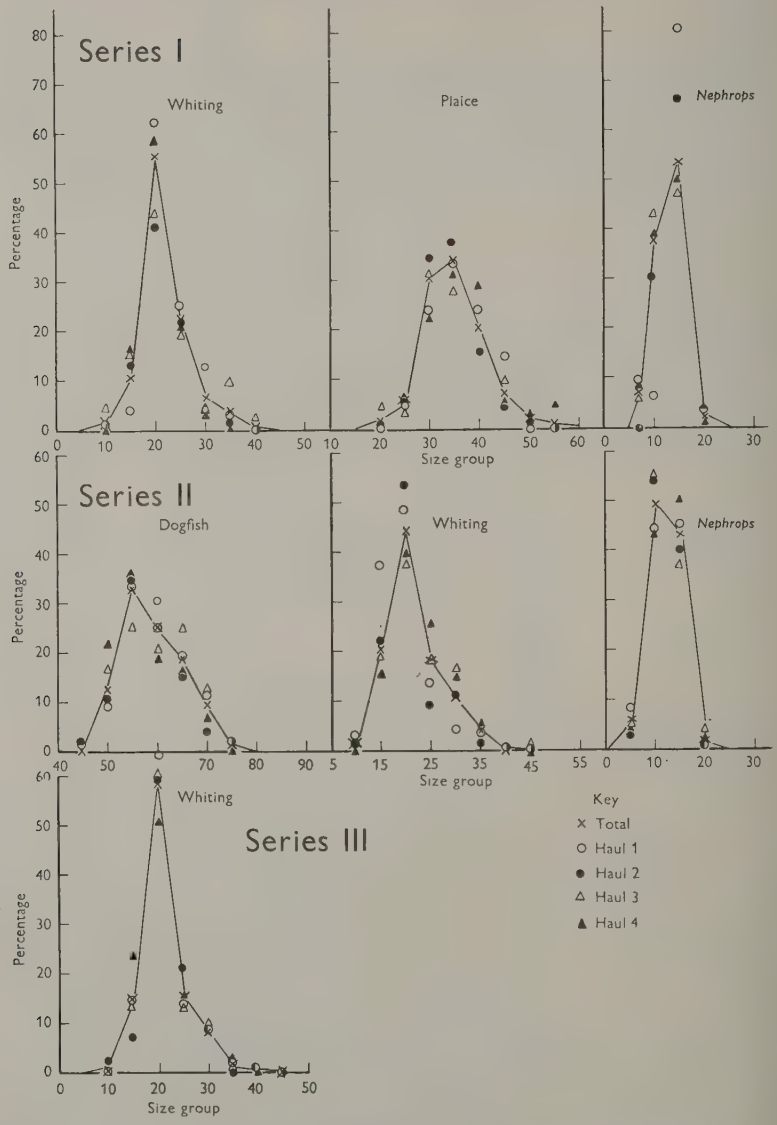

Fig. 3. Percentage frequency distribution of size-groups. Values shown for totals and separate hauls of a given series.

was small and since in others more than one population (as regards size-groups) was sampled in one haul, quantitative deductions regarding size-frequency in sample and in population have not been made. It is clear, however, that the figure and table strongly suggest that a similar population as regards size-distribution was being sampled throughout any given series.

Series I

In series I the species caught in adequate numbers for analysis were the 'round' fish (cod, whiting, poor cod, hake) and the 'flat' fish (plaice, witch, long rough dab) together with *Nephrops*.

In haul 1 of this series a moderate number of haddock was taken (39), although in subsequent hauls the numbers of this fish were very small (2, 3, 0). It is suggested that during part of the first haul a somewhat different ground had been sampled; this suggestion is substantiated both by the occurrence in

TABLE III

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects			
Hauls (H)	3	0·1088	0·0363
Species (S)	3	1·6688	0·5563
Residual			
$H \times S$	9	0·5334	0·0593
Total	15	—	—

TABLE IV

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects			
Hauls (H)	3	0·4521	0·1507
Species (S)	3	0·9466	0·3155
Residual			
$H \times S$	9	0·3985	0·0443
Total	15	—	—

this haul only of large numbers of *Asterias rubens* and *Metridium* sp., indicating somewhat harder ground, and by the echo-sounding records seen in Fig. 1, where the trace of haul 1 is somewhat different. It is therefore of interest to note that the stomach contents of the haddocks caught in this first haul consisted largely of the remains of *Ophiura* sp., indicating hard-ground feeding, whereas in contrast, the stomach contents of the species common to all the hauls correspond to the invertebrate fauna of the sandy mud.

The 'round' fish and 'flats' (together with *Nephrops*) are considered separately. The analysis of variance for 'round' fish is given in Table III. The error variance of a single observation (H is less than $H \times S$) is 0·0593 corresponding to a log standard deviation of 0·2436 or a coefficient of variation of 75·3%, for a given species.

For the second group, 'flat' fish plus *Nephrops*, the analysis is given in Table IV. The mean square for hauls is not significant and an estimate of the error variance is obtained by pooling H and $H \times S$. This gives the variance of a single observation as 0·0708 or a log standard deviation of 0·2663, corresponding to a coefficient of variation of 84·7%.

The catches of *Nephrops* were more irregular than the 'flat' fish, and analysis of the latter separately gives a coefficient of variation of 59·7%. There were large enough numbers of witch in this series to consider two separate size-groups, namely greater and less than 25 cm. An analysis of variance of these two size-groups considered by themselves gives a coefficient of variation of 48·9%.

Series II

In this series, taken 6 days later, there was some change in the major species caught. The hake were negligible, whilst large numbers of spur-dogs were taken. The division into 'round' (which includes the latter) and 'flats' plus

TABLE V

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects			
Hauls (H)	3	0·3293	0·1098
Species (S)	3	1·8083	0·6028
Residual			
$H \times S$	9	0·3596	0·0400
Total	15	—	—

TABLE VI

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects			
Hauls (H)	3	0·1178	0·0393
Species (S)	2	2·1836	1·0918
Residual			
$H \times S$	6	0·1428	0·0238
Total	11	—	—

Nephrops has been maintained. For the 'round' fish the analysis of variance is shown in Table V. Again pooling H with $H \times S$ since the former is not significant, gives a mean square of 0·0574, or a log standard deviation of 0·2396 corresponding to a coefficient of variation of 73·7%.

For the second group ('flat' fish plus *Nephrops*) the analysis of variance is shown in Table VI. The value for H is not significant; pooling gives an estimated error variance of a single observation of 0·0290, a log standard deviation of 0·1703 and a coefficient of variation of 48%.

Series III

In this set dogfish were again absent and haddock were very few, the remaining species being as before, with a noted absence of hard-bottom fauna. Analysis of the 'round' fish is given in Table VII. Again the value for hauls is not significant; the variance of a single observation after pooling is therefore given by 0·0203, a log standard deviation of 0·1425 and a coefficient of variation of 39%.

TABLE VII

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects			
Hauls (H)	3	0·0786	0·0262
Species (S)	2	1·8816	0·9408
Residual			
$H \times S$	6	0·1041	0·0174
Total	11	—	—

TABLE VIII

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects			
Hauls (H)	3	0·0968	0·0323
Species (S)	3	0·5172	0·1724
Residual			
$H \times S$	9	0·3006	0·0334
Total	15	—	—

The analysis with the 'flats' plus *Nephrops* is given in Table VIII. The value for hauls is less than that for interaction so that the latter may be taken as the required error variance; this is equivalent to a log standard deviation of 0·1828 corresponding to a coefficient of variation of 52%.

DISCUSSION

The coefficient of variation, which although in the first instance is strictly applicable only to the present results, has been found to vary from 40 to 85% and this includes values for both 'round' and 'flat' fish. There is no reason, however, to believe that the value is other than adequately representative of this type of sampling of inshore populations. As Winsor & Clarke (1940) pointed out, with such high log standard deviation it is usually better to work on log values throughout, but if 2σ limits are set from these logarithmic values (see Silliman, 1946, for pilchard eggs), then taking 75% as a representative value for the coefficient and converting to actual catches the fiducial limits would be 30–300% for a single observation from a single haul. The catches of a given species from two separate hauls could not, on this basis, be considered significantly different unless one was less than a third or greater than three times the other. In attempting to 'contour' fish populations these limits would also be observed.

The mean catches for all the more abundant species for the three series are given in Table IX. In series I an invasion of haddock into the area, or sampling from a somewhat different ground, has been noted. In the second series there was an incursion of dogfish on to the grounds, the fish being present in reasonable numbers in all four hauls; in contrast to the haddock in series I these dogs were therefore distributed over the whole sampling area. The stomach contents were in an advanced state of digestion, suggesting that they had not been recently feeding on this ground. The cod, whiting, poor cod and hake of the

TABLE IX. MEAN CATCHES OF CHIEF SPECIES IN SERIES I–III

	I	II	III
Dogfish	0	52·3	(1)
Cod	16·5	13·8	16·5
Whiting	74·5	110·0	115·3
Poor Cod	11·0	21·0	(12)
Hake	14·5	(9)	15·8
Plaice	56·5	14·0	42·5
Witch	41·8	(8)	14·5
Long Rough Dab	19·3	15·8	16·0
Nephrops	118·5	120·5	21·3

TABLE X

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects			
Dates (D)	2	0·1423	0·0712
Hauls (H)	3	0·0108	0·0036
Species (S)	3	5·2682	1·7561
First-order interactions			
$D \times H$	6	0·1106	0·0184
$D \times S$	6	0·5190	0·0865
$H \times S$	9	0·2347	0·0261
Residual			
$D \times H \times S$	18	1·1577	0·0643
Total	47	—	—

'round' fish have shown a constant population over the whole sampling period of 4 weeks. This is indicated by the results in Table IX, and confirmed by analysis (Table X), using the catches for the three separate dates.

The second-order interaction is high; none of the first-order interactions are significant, and the mean squares for dates and hauls are not significant. The population can therefore be considered unchanged throughout the period. The small value for hauls indicates that no significant changes took place as a result of successive hauls over the 'same' ground.

The greatest differences are shown in the two 'flat' fishes, plaice and witch, and the crustacean *Nephrops*. The catch of plaice showed a significant fall in series II. Examination showed that the gonads were almost ripe and that the fish had not been feeding; and it was suspected at the time that, as might be

expected at this season, the fish were moving to deeper water for spawning. However, the catches rose again in series III, and this 'recovery' was maintained in later hauls not given. A similar 'recovery' was also found in the witch and *Nephrops*. The reason for these changes is not clear, since when compared with the 'round' fish less mobility would be expected in bottom-living species.

These results give no evidence on the origin of the variability in replicate hauls, that is, how much is due to inadequacies of technique and how much is inherent in sampling variation dependent upon the population distribution. It is of interest to note that as with plankton sampling, the standard deviation is roughly proportional to the mean, whilst the variance is greater than and increases with the mean. This suggests that the population is aggregated into groups, so that much of the sampling variation may be inherent in the population distribution, and this problem is now under consideration.

For ecological work, in order to investigate a particular habitat it may be desirable to sample a large number of small areas in a short time. It was for this reason that half hour hauls were made. Comparison of such short hauls has been made with hour hauls, alternating the order of trawling. In view of the high variability of results it is clear that in order to compare the ratio with that expected (1:2) it is necessary to have a number of counts. Using the results from a number of trawls, with thirty-two separate values of the ratio the mean was 1:1·96. Clearly this value is within the limits expected.

It should be emphasized that the results refer to variations with the *same* gear tested under as far as possible similar working conditions; it might be expected that the variability with a modified gear would be of the same order. The results provide no information regarding the variations which result when different or modified gear is used over the same ground.

Summary

The variability in catch of a series of hauls with a V.D. trawl taken under, as far as possible, controlled working conditions has been determined.

For analysis the species were divided into 'round' fish and 'flat' fish together with *Nephrops*; for both groups the coefficient of variation varied from 40 to 85%. Taking 75% as a representative value, the 2σ fiducial limits are 30–300% for a single species from a single haul of half an hour duration.

It has been found that the standard deviation is roughly proportional to the mean, and that the variance is greater than the mean and increases with the mean. This suggests aggregation of the population.

The species are considered over the whole sampling period (4 weeks). Except for haddocks and dogfish the 'round' fish constituted a constant population. Changes were found in the other groups and their origin is discussed.

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SPONTANEOUS ACTIVITY PATTERNS IN ANIMAL BEHAVIOUR: THE IRRIGATION OF THE BURROW IN THE POLYCHAETES *CHAETOPTERUS VARIOPEDATUS* RENIER AND *NEREIS DIVERSICOLOR* O. F. MÜLLER

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(Text-figs. 1–8)

The water movements by which many polychaete worms irrigate their burrows are easy to record kymographically. It has been shown, by these means, that the common lugworm, *Arenicola marina*, tends to settle down to a characteristic pattern, in which the water is driven in vigorous bursts, separated by periods of gentler irrigation or of rest. The bursts are not reflexly produced, as one might perhaps suppose, by O_2 lack or CO_2 accumulation in the burrow, but are due to a spontaneously rhythmic pacemaker system internal to the worm (Wells, 1949*a*, *b*; Wells & Albrecht, 1951). The experiments to be described were made on polychaetes of other families, to find out whether equally characteristic patterns appear, and, if so, to what extent they depend on external conditions.

Our main interest lies, not so much in the respiratory and feeding mechanisms of the species concerned, as in a more general problem. The irrigation of a burrow is closely akin to locomotion. One has only to consider those Crustacea which swim to filter-feed, rather than to get anywhere, to see how the two are connected. Now the rate of locomotion of an animal varies in response to external conditions, and also, as far as one can see, spontaneously—a fact of which anybody who has attempted experiments on taxes and kineses is aware. Sometimes the variations are very regularly cyclic, as with many medusae. We believe that the study of irrigation rhythms has a useful contribution to make to the wider problem of activity variations in animal behaviour. It has the great advantages, that a water current is easily recorded, and the conditions are easily controlled; the investigator avoids the technical problems set by an animal which moves from place to place.

The experiments were done at the Plymouth Laboratory, in January, March and April, 1950, at temperatures ranging from 11° to 16° C.—those on *Chaetopterus* by G. P. W. and those on *Nereis* by R. P. D. We wish to thank Mr N. A. Holme, who first pointed out to us the suitability of *Chaetopterus* for work of this kind.

Methods

Modified versions of the apparatus previously described for *Arenicola marina* were used.

Method for Nereis

The results on this species were got with a rather generalized apparatus, that would probably give good results with many burrowing polychaetes (Fig. 1, left-hand side).

The apparatus is immersed in a tank of circulating sea water to the level *A*. The worm is in U-tube *B*, whose diameter can be chosen to suit the species to be used. The right-hand end of the U opens into the outer tank, and the left into wide cylinder *C* (internal diameter 31 mm.). The cylinder communicates with the outer tank through capillary *D* (internal diameter about 1 mm.). Owing to the resistance of *D*, the pumping movements of the worm cause slight variations in the level of the sea water in *C*. These are recorded by means of a lever connected to 'float' *E*, made of paraffin wax moulded on to a silver disk (diameter, before thinly coating with paraffin, 29 mm.). The 'float' really sinks, but is held in the required position relative to the meniscus by counterweight *F*. The water movements are traced by frontal writing point *G*.

In certain of the experiments, the circulation was closed, so that the worm had access only to a limited volume of non-aerated water. This can be done by means of a glass T-piece connected to rubber tubes *H*, *I*, *K*; *H* is connected to *B* and *I* to *D*. Tube *K* is 40–50 cm. long and opens into the outer tank. The fitting can therefore be attached without interrupting or defacing the tracing. When this has been done, the worm can circulate the water contained in *B*, *C*, the T-piece and the connecting tubes, but the system is now practically closed. Only very small amounts of O_2 or CO_2 will pass between *C* and the closely fitting 'float'. Recording occurs as before, and the variation in the volume of water in *C* which this entails is compensated by an ebb-and-flow movement in *K*. Owing to the capacity and form of the dead space which the latter presents, there will be little renewal from this source.

Method for Chaetopterus.

The apparatus just described was modified in three respects, as shown on the right in Fig. 1.

(i) Because of the great vigour of the currents produced by *Chaetopterus*, capillary *D* is replaced by glass tube *L*, drawn out to a jet of internal diameter 1·5–2 mm. (ii) Tubing *H* is replaced by the second wide cylinder *M*, to allow of feeding experiments (see below). The level in *M* is held constant by open tube *K*. (iii) The worm is mounted in its own parchment-like tube *N*. The narrow ends of the tube are cut off, and the rest is tied on to a pair of glass tubes, sleeved by rubber tubing of suitable size.

For closed-circulation experiments, cylinder *M* is sealed with liquid paraffin, as shown in the figure. The circulation can now be closed when desired, by passing rubber tube *I* over jet *L*. For feeding experiments, the

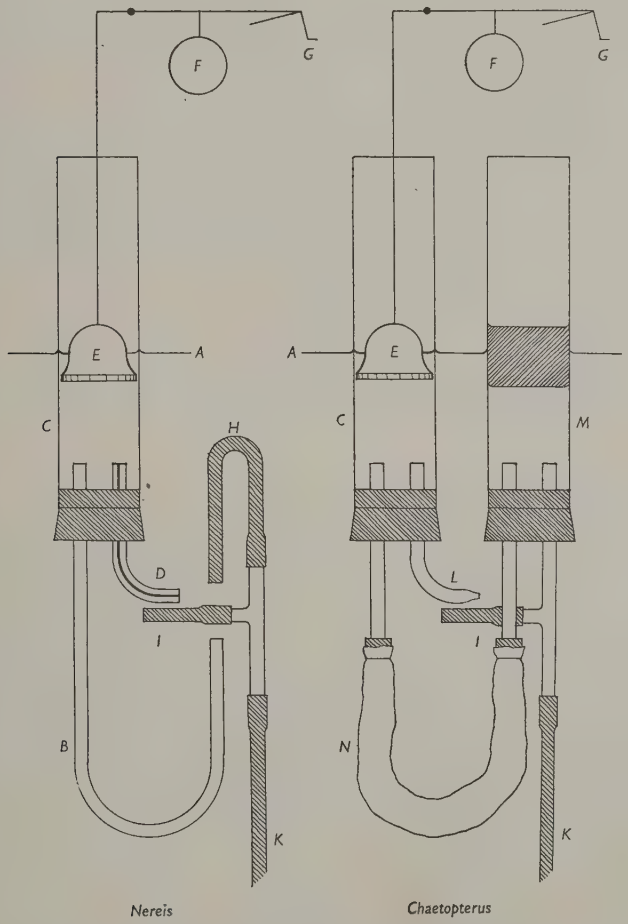

Fig. 1. Apparatus for recording the irrigation currents (see text).

paraffin seal is omitted, *M* is stirred and aerated by an air-jet, and *I* is kept permanently on *L*. The effect of adding diatom cultures, tow-nettings, etc., to *M* can now be recorded.

Calculation of flow rates from the records

The main objective of the experiments was to get a picture of the worm's activity cycles over long periods of time. The records were therefore taken on slowly moving surfaces (at 1 to 6 cm./hr.). This means that they are unsuitable for the measurement of the amounts of water propelled by the worms, except during sustained spells of steady pumping. The general method for deriving flow rates from the tracings is as follows.

(i) *The flow rate through the capillary or jet.* This is proportional to the difference of pressure between the ends of the capillary and therefore to the excursion of the writing point, provided that the temperature is constant and that a certain critical flow rate is not exceeded. We will assume at first that these conditions are satisfied.

The capillary constant j is defined as the flow rate through the capillary in c.c./min. when the pressure difference across it is 1 cm. water. Let amplification factor of lever $= k$, diameter of cylinder $C = d$ cm., velocity of writing surface $= v$ cm./min.

If at any moment the writing point is w cm. from the null position, then the flow rate through the capillary at that moment is

$$\frac{j}{k} w \text{ c.c./min.}$$

If over any period of time the area between the tracing and the null line is a cm.^{2}, then the total flow through the capillary in that period is

$$\frac{j}{kv} a \text{ c.c.}$$

The constant j could be calculated from the equation:

$$j = 25600 \frac{\rho}{\eta} \frac{r^4}{l} \text{ cm.}^2\text{/min.}$$

where ρ, η are respectively the density and coefficient of viscosity of the sea water, and r, l are the radius and length of the capillary in centimetres. In practice, owing to the difficulty of measuring r with sufficient accuracy, the value of j is best determined by setting up the apparatus without a worm, allowing sea water to flow into C through B at a known constant rate (from a graduated Mariotte bottle) and recording the excursion of the writing point. The dependence of j on viscosity necessitates a careful watch on the temperature, not only during calibration but throughout the work, since the Q_{10} of the viscosity of sea water is about 1·3.

At a certain critical flow rate the flow becomes turbulent and the linear relation between pressure and flow rate breaks down. The critical pressure difference h_c necessary to produce turbulent flow is given very approximately in cm. of sea water by the equation

$$h_c = 8 \frac{\eta^2}{\rho^2} \frac{l}{r^3} \text{ cm.}$$

Inserting the following rough but reasonable values: $\eta = 0{\cdot}012$, $\rho = 1$, $l = 5$, $r = 0{\cdot}07$, we get a value of 16·5 cm. for h_c. This is of course very much greater than the height to which the level in C can rise, so we may conclude that the linear relation will always hold when a capillary of dimensions suitable for such worms as *Arenicola* or *Nereis* is on the apparatus. However, h_c falls rapidly with an increase in r, and it also falls (through η) as the temperature rises. Where doubt exists, the linearity of the relation

between pressure and flow rate can easily be checked during calibration. We found that the jets used for *Chaetopterus* gave turbulent flow even under ordinary working conditions, so we derived the flow rates for this worm from curves made by recording the lever excursions at various known flow rates.

The critical flow rate above which turbulence occurs is jh_c c.c./min., and inspection of the above equations shows that this product is proportional to r but independent of l. In other words, when choosing capillaries for recording rapid rates of flow, a long, wide tube should in general be preferred to a short, narrow one giving the same value of j.

(ii) *The output of the worm.* The volume of water in cylinder C varies with the position of the writing point. This means that the output of the worm is equal to the flow through the capillary or jet whenever the tracing is running parallel to the null line. If the two lines are diverging, the worm's output exceeds the return rate through the capillary; if they are converging, it is less.

If at any moment the tracing slopes away from the null line at an angle θ, the worm's output exceeds the flow through the capillary by

$$\frac{\pi d^2 v}{4k} \tan \theta \text{ c.c./min.}$$

The total flow through the worm tube over any period is equal to that through the capillary, if the distance between the two lines is the same at the beginning and end of the period. An increase of δw cm. in the distance between the lines means that the worm pumped, during the period in question, a volume of water which exceeded that flowing through the capillary by

$$\frac{\pi d^2}{4k} \delta w \text{ c.c.}$$

For reasons already given, our records are not suitable for the accurate measurement of the slope of the tracing, or (unless it is running nearly parallel to the null line) of the area under it. We have therefore restricted our calculations to estimates of peak velocities and of amounts pumped during spells of steady activity. To do more than this would require records taken on a rapidly moving surface.

Chaetopterus variopedatus

Chaetopterus variopedatus is a specialized polychaete living in a roughly U-shaped tube of parchment-like material which it secretes. It is generally found below low-tide mark, though in certain localities it can be collected from the lowest part of the beach. The water currents through the burrow are driven by the three muscular 'fans' or 'palettes'. Each fan is derived from the dorsal wall and notopodia of a single segment. The three fans are borne on segments xiv, xv and xvi.

Two published accounts of the movements of the fans are of great importance in the present context. They are by Enders (1909), who described many aspects of the worm's behaviour, and MacGinitie (1939), who gave a detailed account of a method of feeding.

The fans normally drive water in a tailward direction, the only exception so far recorded occurring when irritating matter is being expelled from the tube (see below). The worm can reverse itself very rapidly in the tube, and produce

a change in the direction of flow by this means; according to Enders, turning round can be completed in from 10 to 20 sec.

The main functions of the water currents, as described by Enders and by MacGinitie, will now be summarized.

Feeding. The gut contents include mud and sand particles, diatoms, foraminifera, shells of mollusc embryos, skeletons of copepods and young Crustacea, and eggs of *Chaetopterus* itself (Joyeux-Laffuie, 1890; Enders, 1909). The collection of fine carmine suspensions and of diatoms was watched by Enders, who describes their trapping in mucous strands running along ciliated grooves on certain of the appendages of the anterior end; the strands are carried along a dorsal ciliated groove to the mouth, where they are either swallowed or rejected: 'This has the appearance of a selective response on the part of the cilia.' Further details of the processes of swallowing and rejection are given by Faulkner (1931). A different mechanism is described by MacGinitie, who writes: 'No paper that I have seen has given the correct method of feeding of this animal.' According to MacGinitie, a mucous bag is secreted across the lumen of the tube, and water is driven through the tube for some time, during which suspended particles are filtered out by the bag. The bag is finally rolled up into a bolus, passed along the dorsal ciliated groove to the mouth, and swallowed. A new bag is then secreted, and so on. The following details of the timing of the performance are taken from MacGinitie (1939) and from MacGinitie & MacGinitie (1949): 'From the beginning of the spinning of the mucous bag to the ingestion of the bolus of food required, on the average, 17 minutes, and varied only plus or minus 1 minute from this average'; during filtration, the fans beat about once per second; 'this ceases while the pellet of food is being propelled to the mouth'. Our views on the question whether either method of feeding is more correct than the other are given below.

Expulsion of irritating matter. A number of interesting responses to the introduction of coarse carmine granules or sand are described by Enders. The first response to the presence of such particles in the tube is cessation, then reversal, of the direction of beat of the fans; the headward strokes may be performed 'with such energy that the irritating material is expelled to a distance of several centimetres above the end of the tube'. With more severe stimulation, other responses appear. They result in a tailward expulsion of the particles, the worm reversing itself for the purpose if necessary. Tailward expulsion is sometimes remarkably vigorous: Enders describes the driving of sand up to a water surface 30–45 cm. above the opening of the burrow.

Expulsion of faeces. MacGinitie makes no mention of defaecation, and the following details are taken from Enders. The faecal masses 'are sometimes discharged from the anus singly, but more frequently by twos and threes... they remain until a fairly constant number has been discharged, then the palettes vibrate more strongly and expel them to the exterior. When the small specimens upon which I have made observations were well fed they expelled

from ten to twenty masses at intervals of four minutes. The faeces are expelled with considerable force.' Even if the animal receives very little food, it produces faeces consisting largely of mucus. It is rather remarkable that the forcible performance described by Enders was not recorded by MacGinitie; the point is returned to below.

Other functions. According to MacGinitie & MacGinitie (1949): 'When the worm is not feeding, the fans may beat to supply a current for respiration, but this beating is intermittent and arhythmic.' A comparatively gentle background of activity is apparently adequate to supply O_2 and wash away CO_2 and the nephridial excretions, in the absence of the more vigorous currents described above. As the intestine loops up into each fan, irrigation presumably influences the movement of food along the gut.

Irrigation patterns

Our experiments on *Chaetopterus* were begun at the suggestion of Mr N. A. Holme, who showed us a living specimen which had made its burrow in a glass jar. The jar had been dredged up during an Easter Class excursion, and the worm subsequently lived over a year in one of the aquarium tanks. The circulating sea water in the Plymouth Laboratory therefore contains enough suspended matter to supply the animals' needs.

Our records of worms in their own tubes were taken from twelve individuals each one kept in the apparatus for from 2 to 6 days, and yielding a total of thirty-seven recorded 'worm-days'. Experimental tests (closure of the circulation, feeding) were made from time to time on five of these worms; the rest were left in peace.

Portions of the records are chaotic, but the greater part of the material can be grouped into one or other of four main patterns. Each of these was seen in several worms, and most of the worms gave at least two of the patterns, registering one of them for a few hours and then changing, apparently spontaneously, to another. The patterns are as follows.

(*a*) *Expulsion behaviour* (Fig. 2).

The worm traces brief but very violent outbursts, during which the writing point moves up and down over a wide distance and with impressive speed, its strokes evidently corresponding to the 'kicks' of the fans. Between these bursts the worm is nearly or quite motionless. The bursts may follow each other fairly rapidly (as in the first part of Fig. 2), or at longer, and sometimes rather regular, intervals (as at the end of Fig. 2). The worm often reverses itself while registering this type of behaviour (this occurs four times in the first half of Fig. 2). The quantities of water driven during the outbursts can only be estimated very roughly from the records. The writing point, in the example of Fig. 2, often moved over 2 cm. at each stroke of the fans; this means an increase

of the amount of water in the float chamber, at each stroke, of about 3 c.c. The strokes follow each other at intervals of about a second. We have named this pattern 'expulsion behaviour' because it appears to correspond with the violent ejections of irritating suspensions described by Enders. Its occurrence may be

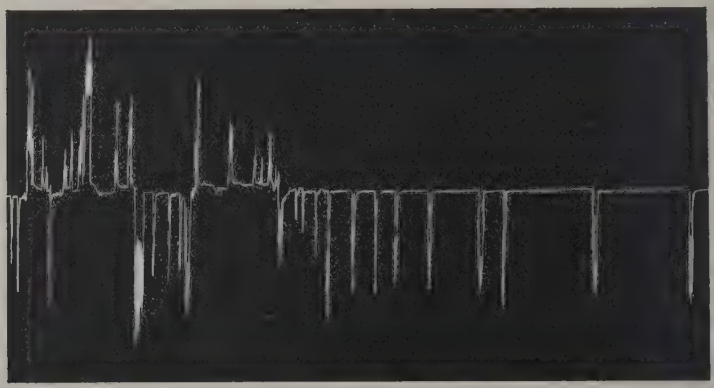

Fig. 2. *Chaetopterus variopedatus*. Irrigation record. The printed extract is 3 hr. long, and begins 1½ hr. after the tube was mounted on the apparatus. *Read all records from left to right.*

due to some disturbing mechanical or chemical factor. It was often seen at the beginning of an experiment, i.e. just after the tube had been tied to the apparatus, but it occasionally appeared later, without evident cause, after the worm had traced other patterns for many hours.

(*b*) *Periodic reversal* (Fig. 3, middle line).

The worm irrigates continuously but rather irregularly, and reverses itself every 20–40 min. This may be a second type of response to irritating conditions, as it appeared very constantly when the circulation was closed (see below), but it often appeared when no evident change in the conditions had occurred. The flow rates in the extract of Fig. 3 gradually fall from about 10 to about 5 c.c./min. In some cases, expulsion outbursts were superimposed on a periodic reversal trace like that of Fig. 3. The first part of Fig. 2 shows periodic reversal in which the continuous irrigation background is very slight compared with the superimposed outbursts.

(*c*) *Mucous-bag feeding* (Fig. 3, upper line).

This pattern was traced from time to time by five of the worms. The base-line is given by the tips of the regularly spaced 'peaks', in the upper extract of Fig. 3. The worm is irrigating very steadily, except for brief pauses at the

'peaks', when the lever returns to the null position. The intervals between pauses average 18 min. The pattern agrees excellently with MacGinitie's account of mucous-bag feeding as summarized above, which it undoubtedly represents. A mucous bag is passed forwards to the mouth and swallowed at each pause. The following quantities can be got from Fig. 3. The flow rate, during the filtration periods, is 16 c.c./min., and the volume of water passed through each bag is about 290 c.c.

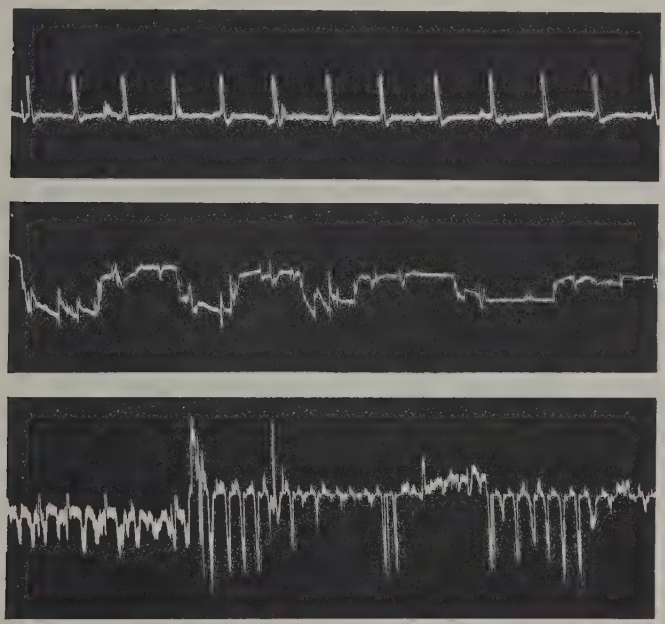

Fig. 3. *Chaetopterus variopedatus*. Extracts from the irrigation records of three individuals, all taken with the same lever magnification factor. Each extract is 4 hr. long.

Unfortunately, the paper was moving too slowly for the individual fan strikes to be counted, but the whole picture agrees so well with MacGinitie's account that his figure, of about 1 stroke per sec., can probably be applied to the activity in Fig. 3. This means that the fans were propelling about 0·27 c.c. of water per stroke, or less than 10% of what they can drive when taking vigorous ejection action.

(*d*) *Five-minute cycle* (Fig. 3, lower line).

There is fairly continuous activity on which a cycle is evidently superposed, having a period of about 5 min. (5·3 min. in the extract of Fig. 3). The cycle

varies somewhat in its expression, as the extract shows, but it often appears as a series of brisk, but by no means maximal, outbursts of the expulsion type. The picture agrees reasonably well with Enders's account of the forcible ejection of faeces from the tube every 4 min., as summarized above.

Now a striking feature of the upper line of Fig. 3 is the absence of anything which could be interpreted as faecal ejection, neither does MacGinitie mention such an act as interrupting the mucous-bag feeding process. On the other hand, the description of Enders is very clear and convincing. The available facts suggest that *Chaetopterus* has more than one method of feeding. We know that *Nereis diversicolor* can take relatively large pieces of animal or plant material with its jawed proboscis, or ingest the surface mud, or filter-feed with a mucous plankton net (Linke, 1939; Harley, 1950); and there seems no reason why *Chaetopterus* should not ring the changes too. Perhaps the MacGinitie method is chiefly

Fig. 4. *Chaetopterus variopedatus*. Irrigation record. The circulation was closed for 3 hr., between the marks *A*. Total length of extract, 10 hr.

used when the suspended particles are few and fine, and the Enders method when they are coarser and more numerous; the first might result in the production of light, mucoid faeces which would drift away with the filtration current, and the latter of heavier ones which would have to be kicked out.

Response to closure of the circulation

As described on p. 663, the circulation could be closed in such a way that the worm had access to only about 90 c.c. of water, including the volume contained in its tube, with little opportunity for the entry of additional O_2 or the escape of CO_2 or other metabolites. This was done in seven experiments, made on four worms, the period of closure varying from 3 to 7 hr.

The effect of closure was to produce a sharp increase in the water currents, which lasted during the whole closure period (Fig. 4). The movements consist in the main of violent expulsion bursts, superimposed on periodic reversal in the tube; that is to say, they suggest a generalized state of irritation rather than

a specific increase of respiratory irrigation. Re-opening of the circulation was invariably followed by a prolonged period in which the water movements were very slight, or even ceased altogether.

These responses afford a great contrast to those of *Arenicola marina*, as described elsewhere (Wells, 1949*a*). The lugworm irrigates its tube in powerful bursts. If the circulation is closed, the bursts appear with about the same timing as before, but with greatly diminished vigour, and they now seem to serve as a periodic testing of the conditions. When the circulation is opened again, the irrigation is enormously increased, as if the animal were paying off an oxygen debt run up during the period of closure. Now the lugworm typically inhabits tidal sand and mud flats. At low tide, the burrows may lie exposed for hours, and, on a hot summer day, the surface water which often covers them may warm up to temperatures high enough to injure the worm (Linke, 1939; Wells, 1949*a*). An automatic acceleration of irrigation in response to O_2 shortage or CO_2 accumulation would be harmful under these conditions; but the ability to suspend external respiration for some hours, together with testing behaviour when conditions are unfavourable, followed by compensatory hyper-irrigation when the returning tide removes the danger, would clearly tend towards survival. *Chaetopterus*, on the other hand, though it sometimes occurs in the lower part of the tidal zone, is typically found at greater depths, and will seldom, if ever, be exposed to these dangers. The circulation through its burrow might become closed from various causes, such as the settling of some object over the two openings of the burrow. Should this occur, it will be better for the worm to respond in such a way as to remove the obstruction, or to minimize its effects, rather than to wait until the situation should mend itself.

Response to 'feeding'

The effect of adding small volumes of dense suspensions of organisms, by the means described on p. 663, was tried three times, on two worms. A typical response is shown in Fig. 5, when the addition consisted of tow-nettings (from which the larger organisms had been removed with a 1 mm. screen) enriched with diatom cultures (*Biddulphia sinensis*, *Thalassiosira gravida*, *Coscinodiscus centralis*, *Nitzschia closterium*). A prompt and sustained increase in activity can be seen, but the patterns do not resemble those identified above with feeding. They consist in the main of expulsion outbursts. Similar effects were produced by diatoms alone. The type of response suggests that the added organisms were simply irritating, like the sand or coarse carmine in Ender's experiments. Confirmation comes from a single experiment in which a very similar response to that shown in Fig. 5 was given to a suspension of Kieselguhr. Perhaps our additions resulted in too great a density of suspended matter. As already stated, the water circulating in the Plymouth tanks contains sufficient particles to keep *Chaetopterus* alive for over a year.

Dependence of the patterns on external conditions

The following conclusions can be drawn from the results described above.

(i) *Chaetopterus* can exhibit any one of several characteristic irrigation patterns.

(ii) Its choice of pattern at any time depends, to some extent at least, on external conditions. There is evidence that the expulsion bursts, and periodic reversal, appear as responses to irritation. It was suggested, in discussing feeding, that at least two methods of collecting particles are available, and that the particular method employed may be influenced by the nature of the suspended matter in the water.

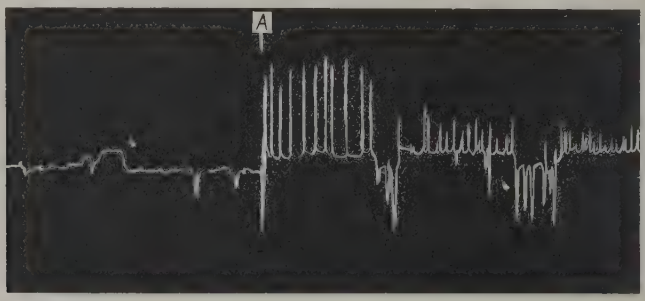

Fig. 5. *Chaetopterus variopedatus*. Irrigation record. A suspension of organisms was added at *A*. Total length of extract, 10 hr.

(iii) Though the choice of pattern can be environmentally determined, intrinsic factors are largely responsible for the forms of the patterns themselves. Periodic reversal appears whenever the circulation is closed, but there is no periodic change in the external conditions which would account for each act of reversal. We seem to be concerned here with the release of an internal rhythmic pattern during the period of action of a constant irritant. The lower line of Fig. 3 strongly suggests that a spontaneous pacemaker is at work, discharging every 5·3 min., but producing movements whose vigour varies from time to time, much as the vigour of the movements evoked by the oesophageal pacemaker of *Arenicola marina* can vary (Wells, 1937*a*). The very regular and invariable pattern which is traced during mucous-bag feeding, as in the upper line of Fig. 3, again suggests the existence of an internal, spontaneous timing mechanism.[1]

[1] During filtration, the bag is continually being secreted round its rim by the aliform notopodia, and rolled up at its apex by the dorsal cupule, in which its substance collects as a pellet. The timing of the cycle might here depend on a relation between secretion rate and the capacity of the cupule.

Behaviour of isolated fan segments

The complex irrigation patterns could conceivably be due to the modulation of a simple inherent rhythmicity of the fan-bearing segments by influences coming from other parts of the worm. To test this possibility, we took a number of records from single fan segments. It was already pointed out by Berrill (1927) that isolated fan segments will beat in sea water for 4 or 5 weeks, and that their movements depend on the presence of the nerve ganglia. In our experiments, the worm was ligatured in front of one of the fans, the ends of the thread were tied into a loop, and the segment was isolated by transecting the worm in front of the ligature and behind the fan. The preparation was mounted in sea water, by passing the loop over a horizontal glass rod, and a fine hook passed through the tip of the fan was connected to a light isotonic lever (pull on the preparation, 0·4 g.).

Segments set up in this way remain vigorously active for at least 24 hr., but their behaviour is surprisingly variable. The extracts in Fig. 6 show not only several behaviour-rhythms of different frequencies, but also striking and apparently spontaneous changes of pattern. The sudden increase in activity, seen in the last third of the upper extract, is a typical example.

Accustomed, as one becomes in the classroom, to the steady performance of such material as the heart of the frog, or the gill cilia of *Mytilus*, one naturally looks for external causes to explain these sudden changes of pattern. However, if two or three isolated segments are recorded simultaneously, in the same vessel of sea water, they change their patterns at different times, and quite independently of each other. If external causes were responsible, their behaviour might be expected to be parallel. The causes of the fluctuations are apparently internal to the preparations themselves.

The isolated oesophagus of *Arenicola marina* exhibits at least three types of spontaneous activity: (i) a simple rhythmic alternation of contraction and relaxation, following each other at intervals of a few seconds; (ii) cyclic alternation of periods of rhythmic activity and periods of rest, the whole cycle lasting for a few minutes; (iii) superimposed disturbances, often coming very regularly at intervals of the order of 1 hr. (Wells, 1937*a*; Wells & Albrecht, 1951). At least the first two of these are functionally normal, and not experimental artefacts. Perhaps the changes of pattern shown in Fig. 6 would appear cyclically, if the preparations could be kept going for many days and recorded on even slower drums. In any case, the segments evidently show spontaneous behaviour patterns of much greater elaboration than those shown by isolated hearts, and the same is true of many invertebrate preparations, including extroverts and body-wall strips of several polychaete species (Wells, 1937*b*, 1939; Wu, 1939; Wells & Ledingham, 1940). It may be the simple regularity of the heart which is the more specialized, since it has obvious functional value.

We have not traced any detailed correspondence between the time-patterns

of the isolated fan segments and those of the intact worm; but it seems clear that the former afford a good supply of material from which the latter could be constructed. There is also, of course, the likelihood of other spontaneous centres, elsewhere in the nervous system.

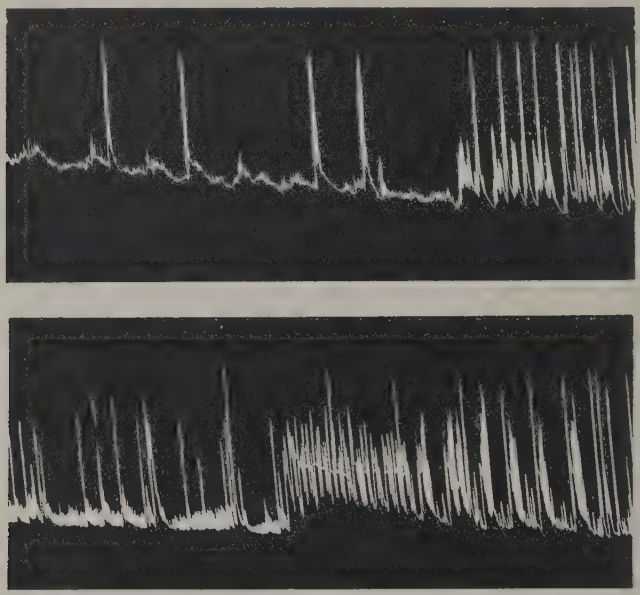

Fig. 6. *Chaetopterus variopedatus*. Movements of the isolated 14th segment, recorded with a light isotonic lever. Each extract is from a different individual. Duration of extracts, 4 hr.

Nereis diversicolor

Our experiments on *Nereis* arose from the coincidence at Plymouth of R. P. D., who was studying the ecology of this species, and of G. P. W., who was completing the work on *Chaetopterus*. A small number of records were taken from *Nereis*, to compare (*a*) its irrigation patterns in aerated sea water, and (*b*) its responses to closure of the circulation, with those of *Arenicola* and *Chaetopterus*.

Unlike *Chaetopterus*, *Nereis diversicolor* is almost entirely restricted to the littoral zone. It lives in mud or sand, in a fairly permanent burrow; this may be a simple U, but often it is complicated by the presence of additional branches with openings to the surface (Linke, 1939).

Until recently *N. diversicolor* was described as feeding partly on such objects as algal fragments and dead Crustacea or molluscs, and partly by swallowing the

surface mud around the opening of the burrow (Thamdrup, 1935; Linke, 1939). The water current, which it drives through its burrow, was therefore mainly respiratory; as a secondary function, it could bring chemical stimuli to the worm, and so inform it of the presence of suitable food (Copeland & Wieman, 1924). Browsing on the mud has frequently been watched by R. P. D. on many beaches, and is undoubtedly of great importance. However, Harley (1950) has shown that the worm can also use a filter-feeding mechanism, like that of *Chaetopterus*, in which water is driven through a mucous net across the burrow. Harley's observations were made on worms in glass tubes, as ours were; there is as yet no information about the importance of the process in the everyday life of the animal.

The waves producing the irrigation current are dorsiventral, while those which accompany locomotion are lateral. It follows that irrigation must be interrupted by acts involving locomotion, such as the backward excursions to the surface for defaecation. Apart from this, the irrigation of worms in glass tubes is always intermittent, periods of undulation alternating rather irregularly, and without visible cause, with periods of rest.

The irrigation waves invariably travel along the body in a head-to-tail direction. The worm can turn rapidly round in the tube, and so reverse the direction of the water current.

Irrigation patterns on open circulation

Our material was obtained from 4 worms, recorded continuously for 21, 22, 39 and 42 hr. The circulation was closed twice with one worm, for 4 and $7\frac{3}{4}$ hr., and once in each of the others, for $10\frac{1}{2}$ and $12\frac{1}{2}$ hr.

The irrigation of the worms, on open circulation, was never steadily sustained, but consisted of short bursts, between which the lever usually returned momentarily to the base-line. In two worms irrigation was often interrupted by periodic rests of about 10–15 min. duration; several such rests are seen in the 3 hr. before the circulation was closed in Fig. 7. They are reminiscent of the pauses studied by Lindroth (1938) and by van Dam (1937, 1938) in *Nereis virens*, but their timing is rather different from that which Lindroth gives as typical for the latter species. 'Ventilationsperioden von etwa 5 Minuten Länge' he writes 'werden von Ruheperioden von 20 bis 30 Minuten abgelöst', whereas in our own records the pauses are relatively brief interruptions of irrigation.

All of the worms showed spells, of several hours' duration, during which the pattern reversed itself at intervals of 15 to 45 min.; examples of this periodic reversal, which is due to the worm turning in the tube, are seen at the beginning and end of Fig. 8. This might be a response to unfavourable conditions, as in *Chaetopterus*; on the other hand, if the water current serves for chemical testing of the surroundings of the burrow, it will clearly be of advantage for each of the openings to act in turn as a nostril.

The filter-feeding of *Nereis*, as described by Harley (1950), is very much less regular than that of *Chaetopterus*. The process of secreting a mucous net, driving water through it, and then swallowing it, may take anything from a little over 1 min. to nearly 7 min., according to her figures, and she writes: 'The cycles of feeding may follow rapidly one after the other with a few short breaks, or they may occur with intervals of several minutes, or irregularly, for a total period of about two hours.' Some of the rapid oscillations in our tracings—for instance, those which occur in a continuous series, about one-third of the way across the upper part of Fig. 8—might be due to this cause, and it is difficult to see what other functional significance they could have; but the pattern as described by Harley is so variable, that the identification cannot be made with any certainty.

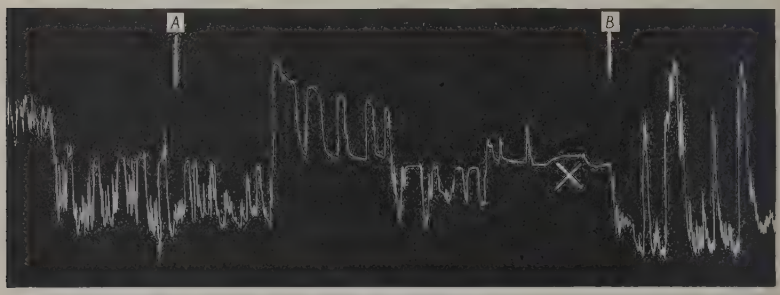

Fig. 7. *Nereis diversicolor*. Irrigation record. The circulation was closed between *A* and *B*. Total length of extract, 22 hr.; length from *A* to *B*, 12½ hr. The slight rise at *X* is an artefact due to a temporary change in level of the water in the outer tank.

It will at least be clear, from the illustrations, that there are several distinct behaviour patterns in this species, and that, as in *Chaetopterus*, they may suddenly replace each other without evident external cause. Moreover, the patterns traced by *Nereis* are different from those of *Chaetopterus*, or of *Arenicola*. It is as if each species had its own handwriting.

Response to closure of the circulation

The response of *Nereis diversicolor* to closure of the circulation is as follows. There is little change in behaviour for 2–3 hr., then the rapid activity oscillations are replaced by long spells of relatively steady irrigation separated by equally long, or longer, periods of complete rest. Irrigation activity gradually decreases, and after many hours of closure it has fallen practically to zero (Figs. 7, 8). Re-opening of the circulation is followed by a prompt resumption of irrigation, and the amounts of water passed are well above normal for a considerable time.

The sudden change of pattern produced by closure, shown very clearly in Fig. 7, is arresting. Evidently, the outbursts of irrigation cannot be direct responses to O_2-exhaustion or to CO_2-accumulation in the tube, for after closure the irrigation would then become more and more powerful, and more and more continuous, and it would rapidly decrease on re-opening the circulation. We seem to be concerned once again with the sudden release, under the closure conditions, of a pattern whose detailed characteristics are part of the make-up of the worm.

The responses to closure and re-opening are on the whole similar to those of *Arenicola* and opposite to those of *Chaetopterus*. The difference in reaction between those species was related above to their difference in habitat, and it is

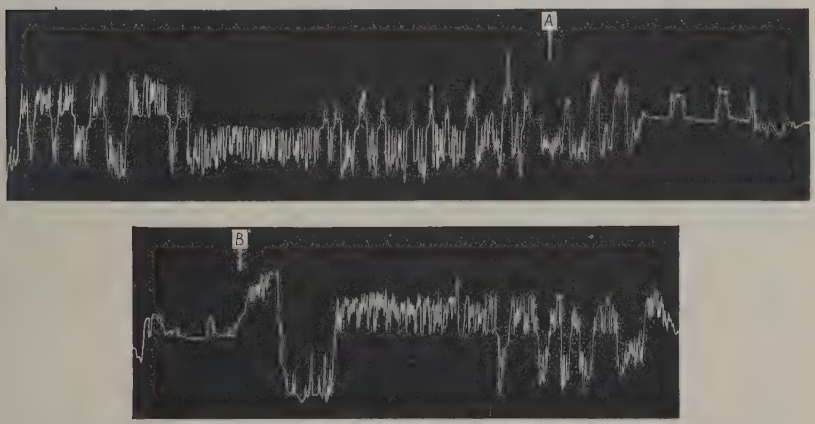

Fig. 8. *Nereis diversicolor*. Irrigation record. The circulation was closed between *A* and *B*. Total length of extract, 38 hr.; length from *A* to *B*, 10½ hr.

at first sight tempting to accept as confirmation the fact that closure depresses, while re-opening increases, the irrigation of *Arenicola* and *Nereis*, both of which are inhabitants of littoral sand and mud flats. On reflexion, however, it will be seen that the agreement is not really so good. *Arenicola* responds to closure, not by a complete change of pattern, but by an immediate reduction in the amount of water pumped at each irrigation outburst. In *Nereis*, on the other hand, large amounts of water are pumped through the burrow in the sustained irrigation outbursts before activity dies away. Clearly, an interpretation in terms of the avoidance of dangerous surface water (as was advanced for *Arenicola*, on p. 671) is inadmissible. Now *Nereis diversicolor* is exceptionally resistant to adverse conditions. Its powers of osmoregulation are well known; its long survival under conditions of practically complete oxygen lack was described by Hecht (1932); and, in the matter of temperature, Linke (1939)

writes of worms that were seen crawling and swimming in surface pools at 30–35° C., though they could have cooled themselves to 20° C or less by simply withdrawing into the underlying mud. These facts suggest that *Nereis* could safely irrigate a burrow when *Arenicola* on the same beach could not, and so its failure to respond to adverse conditions, as *Arenicola* does, by a prompt cutting down of irrigation becomes more intelligible.

Specificity of the irrigation patterns

A more detailed functional interpretation of the irrigation patterns of *Nereis* is hardly possible at present, because the behaviour and conditions of life of the worm in its natural habitat are insufficiently well known. In any case, we are in some doubt as to the extent to which the principle that behaviour is adjusted to habitat can usefully be pressed.

An analogy can perhaps be drawn between the time-patterns which form the subject of this paper, and the space-patterns with which the morphologist and the systematist are concerned. Considering, for example, the variations of shape of the parapodium in polychaetes, one finds a number of obviously adaptive modifications, such as the fans and suckers of *Chaetopterus*, the elytra of *Aphrodite*, or the ring-like parapodia which embrace the more anterior segments of *Arenicola*. On the other hand, the species, especially in the errant families, are often distinguished by slight but constant differences in the proportions of the various parts of the parapodium to which, in spite of their elegance and their value to the systematist, a functional interpretation can hardly be attached. In the same way, though there are certain fairly clear fitnesses in the irrigation patterns (for instance, the 3-phase outburst of *A. marina* serves to integrate the irrigation of the burrow with the periodic defaecatory excursions, and can be converted, in certain circumstances, to a method of aerial respiration), the finer peculiarities which distinguish the tracings of one species from those of another (such as the particular frequency with which a filter-feeding *Chaetopterus* or *Nereis* replaces its mucous nets) may well be functionally meaningless. The metaphor was used above, that each species has its own handwriting, and the detailed characteristics of a handwriting are only of use in establishing the identity of the writer.

Summary

Simple methods for recording the water currents, which many polychaetes drive through their tubes, are described. The circulation may be either open (the worm having access to large amounts of well-aerated sea water) or closed (in which case the worm can circulate a small volume only, and there is no oxygenation or removal of excretory products).

When on open circulation, both *Chaetopterus variopedatus* and *Nereis diversicolor* often trace quite regularly cyclical patterns for hours at a stretch.

Each species has several possible patterns, and may change from one to another without evident external cause. The tracings of each species differ from those of the other, and also from those of *Arenicola marina*, which were described elsewhere.

The details of the patterns traced, on open circulation, by *Chaetopterus* and by *Nereis* are described, and their functional significance is discussed, in the text.

The effect of closure of the circulation is quite different in the two species. *Chaetopterus* responds by an increase in irrigation, the particular patterns traced suggesting a generalized reaction to irritating conditions rather than a specifically respiratory one. *Nereis* responds, first by the appearance of a special pattern (in which long spells of steady irrigation alternate with equally long, or longer, periods of rest), and then by the gradual decrease, which may lead to total cessation, of irrigation.

If the circulation is re-opened after a period of closure, *Chaetopterus* responds by a great decrease, or total cessation, of irrigation, while *Nereis* responds by a prompt return of irrigation activity, the amounts of water pumped being at first much greater than normal.

The movements of isolated fan segments of *Chaetopterus* were recorded with light isotonic levers. They give complicated tracings in which several periodicities can be detected, and they may suddenly, and apparently spontaneously, change their pattern during the course of an experiment.

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THE RESPIRATION OF SOME PLANKTONIC COPEPODS

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(Text-figs. 1, 2)

The respiratory rates of zooplankton organisms are of considerable interest, if only in so far as they permit an assessment of the metabolic requirements of the zooplankton, which forms a vital link in the economy of the sea. Yet very little information is available on the respiratory rates even of copepods, which usually comprise the bulk of a zooplankton community. Data exist only for a few species of copepods, and even then only for a few stages in the life histories of the species. The first measurements of the respiration of a selected species, as distinct from mixed plankton catches, were made by Marshall, Nicholls & Orr (1935). They worked with *Calanus finmarchicus* (Gunner), adults (male and female) and Stage V. In 1939, Clarke & Bonnet published a further series of measurements of the respiration of Stage V *C. finmarchicus*, giving figures slightly higher than those of Marshall *et al.* Zeuthen (1947) included some observations on copepods in his study of size and metabolic rates, but he determined the species of only a few of the animals he used.

In this paper the study of respiration in the Copepoda has been extended to a species much larger than *Calanus*, viz. *Euchaeta norvegica* Boeck, and to two smaller species, *Centropages typicus* Kroyer and *C. hamatus* (Lilljeborg), and in the two larger species, *Calanus* and *Euchaeta*, an additional copepodite stage has been included. In this and further papers a survey will be made of the respiration of the more important species of planktonic copepods, throughout their life histories and under varying environmental conditions. In this way, in time, a picture may be built up of the food requirements of the planktonic population in the sea.

The authors would like to thank Mr E. Ford, the Director of the Marine Station, Millport, for his interest and encouragement in the work.

Material and Methods

Copepods were taken by townet in the Fairlie Channel, or off Garroch Head, both grounds within half an hour's run from the laboratory. The tow-nettings were well diluted for transport. In the laboratory, with the larger forms,

vigorous specimens of the desired species and stage were picked out as soon as possible and put in jars of sea water filtered through Whatman No. 1 filter-papers. The labour of sorting individually large numbers of *Centropages hamatus* was very great; and for them, after the larger copepods and any possible predators such as medusae had been picked out, the townettings were well diluted with filtered sea water, and the *Centropages* picked out only as required. The jars were kept in a sink of running water where the temperature rarely changed by more than 1° C. in 24 hr. No copepods were used until at least the day following capture. An attempt was made not to use the same catch for more than 2 days, but unfortunately rough weather prevented fresh hauls being taken on several occasions, and, especially at the end of the experiments, copepods had to be used that had been captured 4–5 days before.

Respiration was measured manometrically, in Dixon-Haldane constant pressure respirometers, the apparatus being arranged as outlined by Dixon (1943). Clarke & Bonnet (1939), who used this apparatus for their measurement of the respiration of *Calanus*, found that the presence or absence of KOH in the flasks had no effect on the readings observed. We were not satisfied on this point and KOH was always used in the annular cup in the neck of the flask. The respiration flasks were completely immersed in a bath of running water, as no means of maintaining a water-bath at constant temperatures below room temperature was readily available. It was possible by this means to keep the temperature well below 20° C. The maximum range of temperature observed in the bath during any experiment was 0·5° C., which was sufficiently constant to have no disturbing effect on the accuracy of the readings. The greatest disadvantage of this arrangement was the day-to-day variation in the temperature which fell more or less steadily from 19° C. at the beginning of the series of experiments to 15·5° C. towards the end.

The respirometers were attached to a Barcroft shaking-apparatus and shaken with an amplitude of 2 cm. at a frequency of 100 per min. Contrary to the observation of Clarke & Bonnet (1939), this shaking appeared to have no ill effect on the copepods, which survived well—only 10 out of a total of over 600 copepods used in the experiments died during the experiment, and the vast majority of them were alive and active the day following the experiment in which they had been used. However, in view of Clarke & Bonnet's experience, copepods were never used a second time for normal experiments. After closing the respirometer taps, readings were made every 30 min. for 3 hr. and the total change was converted to volume of dry gas at N.T.P. In the first nine measurements, where the respirometer taps were closed 5 min. after the flasks had been attached, as recommended by Dixon, it was found that the first reading of the manometer, 30 min. after the taps were closed, showed a very large change—sometimes two or three times that found for the subsequent 30 min. periods. The period of equilibration was therefore increased to 15 min., and the large initial change was eliminated. In the early experiments where the

equilibration period was only 5 min., and an abnormally large change was recorded in the first 30 min., the first half hour has been neglected and the calculations have been based on the last $2\frac{1}{2}$ hr. experiment.

The respiration flasks usually contained 5 ml. of filtered sea water, but the number of copepods varied with their size—usually 2–5 *Euchaeta*, 10 *Calanus* (adults, Stage V and Stage IV), 20–25 *Centropages typicus* and 50 *C. hamatus*.

For each experiment the copepods were picked out of the jars by eye, but when there was any doubt in identification they were checked under a low-power microscope before being counted into the respiration flasks. In the experiment with *C. hamatus*, in order to save time and damage to the animals, they were sorted by eye only, but were fixed in formalin at the end of the experiment for checking and counting. Any animals which were to be measured after an experiment were similarly fixed and measured with an eyepiece micrometer.

Results

In all, sixty-five separate determinations of respiration were made, and results are listed in Table I. In the table, the fifth column gives the amounts of oxygen in microlitres consumed by one copepod in 1 hr., for the temperature at which the experiment was made. A correction for temperature was made from the curve of respiration of *Calanus* with temperature, given by Marshall *et al.* The sixth column shows the data for respiration corrected to 17° C. Table II gives the mean values for each of these groups of observations, together with the standard deviation of the observations from their mean; the second figure in each pair is that obtained from the data corrected to 17° C. In the discussion which follows reference will be made only to the figures corrected to 17 °C.

More determinations were made on the respiration of *Calanus* Stage V than on any other form, and they include two small groups in which the conditions were changed. In the first special group (Exps. 36–39) the experiments were conducted in the dark, and in the second (Exps. 40–42) the respiration flasks were not shaken at all during the experiment. The group of experiments done in the dark give a mean respiration rate of 0·54 μl./cop./hr. as compared with 0·53 μl./cop./hr. for those in the light; there is no significant difference between these two means ($d/\sigma_d = 0{\cdot}11$). This confirms the finding of Marshall *et al.* that the respiration of *Calanus* Stage V is not affected by light. The mean respiration rate when the respirometers were not shaken was 0·67 μl./cop./hr.; this is significantly higher than that for the rest of the measurements ($d/\sigma_d = 3{\cdot}14$). The number of observations on *Calanus* adult males and on the stages of *Euchaeta* was severely limited by the difficulty of obtaining material; nevertheless, it was decided that the data obtained were worth including.

It has already been explained that, owing to the difficulty of identifying rapidly the stages of *Centropages*, almost all the experiments on *C. hamatus*

Table I. List of Experiments and Respiratory Rates Obtained

Exp. no.	Number and stage	Date	Temp. (° C.)	Respiratory rate (μl./cop./hr.)	Corrected respiratory rate (17° C.) (μl./cop./hr.)
		Euchaeta norvegica			
1	2 adult females	15. ix.	15·85	4·284	4·785
2	4 adult females	10. ix.	16·35	3·077	3·277
3	4 adult females	10. ix.	16·35	2·999	3·194
4	4 Stage V	15. ix.	16·0	2·137	2·351
5	5 Stage V	15. ix.	15·85	2·326	2·598
6	2 Stage IV	15. ix.	16·0	1·069	1·175
		Calanus finmarchicus			
7	10 adult females	27. viii.	18·95	(0·429)	(0·362)
8	8 adult females	8. ix.	16·65	0·759	0·785
9	7 adult females	8. ix.	16·65	0·751	0·777
10	9 adult females	11. ix.	16·0	0·728	0·801
11	10 adult females	11. ix.	16·0	0·967	1·064
12	6 adult males	8. ix.	16·65	0·841	0·870
13	10 Stage V	24. viii.	19·0	0·550	0·426
14	,,	24. viii.	19·0	0·513	0·431
15	,,	24. viii.	19·0	0·844	0·708
16	,,	25. viii.	18·9	0·735	0·622
17	,,	25. viii.	18·9	0·478	0·404
18	,,	25. viii.	18·9	0·542	0·458
19	,,	26. viii.	18·8	0·512	0·437
20	,,	26. viii.	18·8	0·505	0·432
21	,,	26. viii.	18·8	0·551	0·471
22	,,	28. viii.	18·25	0·645	0·577
23	,,	28. viii.	18·25	0·615	0·550
24	,,	28. viii.	18·25	0·676	0·571
25	,,	30. viii.	18·2	0·615	0·552
26	,,	30. viii.	18·2	0·717	0·644
27	,,	30. viii.	17·9	0·521	0·479
28	,,	30. viii.	17·9	0·613	0·568
29	,,	30. viii.	17·9	0·490	0·451
30	,,	31. viii.	17·8	0·493	0·458
31	,,	31. viii.	17·8	0·524	0·486
32	,,	31. viii.	17·8	0·585	0·544
33	,,	1. ix.	17·5	0·643	0·614
34	,,	1. ix.	17·5	0·487	0·466
35	,,	1. ix.	17·5	0·548	0·525
36	,,	1. ix.	17·5	0·609	0·583 Dark
37	,,	1. ix.	17·5	0·457	0·437 Dark
38	,,	1. ix.	17·5	0·579	0·553 Dark
39	,,	2. ix.	16·9	0·578	0·583 Dark
40	,,	9. ix.	16·4	0·682	0·722
41	,,	9. ix.	16·4	0·617	0·654
42	,,	9. ix.	16·4	0·586	0·621 Dark
43	15 Stage IV	6. ix.	17·9	0·262	0·242
44	,,	6. ix.	18·0	0·198	0·180
45	,,	6. ix.	18·0	0·187	0·170
46	,,	11. ix.	16·0	0·270	0·297
47	,,	14. ix.	15·9	0·326	0·362
		Centropages typicus			
48	32♀	8. ix.	16·55	0·317	0·332
49	18♀	9. ix.	16·2	0·273	0·295
50	12♀, 5♂, I..V	9. ix.	16·2	0·222	0·240
51	9♀, 4♂ I..V	9. ix.	16·2	0·308	0·332
52	25♀	12. ix.	15·9	0·167	0·186
53	25♀	12. ix.	15·9	0·158	0·175
54	20♀	13. ix.	15·6	0·187	0·215
55	20♀	13. ix.	15·6	0·172	0·187
56	20♀	14. ix.	15·8	0·169	0·190
57	20♀	14. ix.	15·8	0·110	0·124
58	29♀	14. ix.	15·9	0·222	0·247
		Centropages hamatus			
59	26♀ 10♂, 64 V	2. ix.	16·85	0·079	0·082
60	17♀	2. ix.	16·85	0·125	0·135
61	13♀, 16♂, 31 V	2. ix.	16·85	0·066	0·068
62	15♀, 11♂, 29 V	5. ix.	17·25	0·107	0·105
63	35♀, 5♂, 17 V	5. ix.	17·25	0·112	0·110
64	22♀, 7♂, 5 V	6. ix.	18·0	0·118	0·108
65	15♀, 8♂	8. ix.	16·55	0·134	0·140

and the earlier ones on *C. typicus* were done on groups of animals which included adult males, females and Stage V. The data concerning *C. typicus* fall into two well-marked groups, but for reasons other than this mixing of adults and Stage V. Exps. 48–51 and 58 form one group in which there is a range in the rate of respiration from 0·24 to 0·33 μl./cop./hr. (mean = 0·29), and Exps. 52–57 form a second group in which the rate of respiration is much lower, ranging from 0·12 to 0·22 (mean = 0·18). This difference in respiration rate cannot be explained as a consequence of a difference in the proportionate number of adult and Stage V animals used in the different experiments, since in Exps. 48, 49 and 58 of the first group, and in all the Exps. 52–57 of the second group, the animals were exclusively adult females, yet the rate of respiration was high in the first group and low in the second. Or again, within the first

TABLE II. MEAN VALUE OF RESPIRATORY RATE

		Respiratory rate (μl.O_2/cop./hr.)		Standard deviation σ	
Species	Stages	Observed	Corrected to 17° C.	Observed	Corrected to 17° C.
Euchaeta norvegica	Adult ♀	4·284	4·785	—	—
	Adult ♂	3·038	3·235	—	—
	V	2·232	2·474	—	—
	IV	1·069	1·157	—	—
Calanus finmarchicus	Adult ♀	0·801*	0·857	0·111	0·139*
	Adult ♂	0·814	0·870	—	—
	V (13–35)	0·578	0·517	0·089	0·080
	V (36–39)	0·556	0·539	0·067	0·069
	V (13–39)	0·578	0·521	0·090	0·076
	V (40–42)	0·628	0·666	0·049	0·051
	IV	0·249	0·250	0·057	0·081
Centropages typicus	A (48–51, 58)	0·268	0·289	0·031	0·044
	B (52–57)	0·161	0·180	0·025	0·030
C. hamatus		0·106	0·107	0·025	0·026

* Omitting Exp. 7.

group itself, the rate of respiration in Exps. 50 and 51 in which animals were not all adult females was not significantly different from that in Exps. 48, 49 and 58 in which only adult females were present.

Originally it was thought that the lower rate of respiration in the second group of experiments might be due to starvation of the copepods used, with a consequent reduction in metabolism. In the first four, Exps. 48–51, the measurements of respiration were all made on animals caught during the previous day, whereas in Exps. 52–57 carried out on 12–14 September, the animals used had been caught on 10 September. Those used in Exps. 52 and 53 had been kept for 48 hr. in filtered sea water and had therefore not fed for this period; those in Exps. 54 and 55 had been picked out of the diluted townet catches that had been standing in running water for 72 hr., and although there may have been some phytoplankton in the diluted townetting for the copepods to eat, the

amount may well have been inadequate. The animals used in the four experiments, Exps. 52–55, were therefore transferred to a jar containing a thick suspension of a culture of *Chlamydomonas* and on the following day, after having been fed for 20 hr., the most active of these were picked out and used for Exps. 56 and 57. At the same time Exp. 58 was carried out with fresh animals picked out from a townetting taken the previous day (i.e. 13 September) and fed for 20 hr. The respiration rates in Exps. 56 and 57 were no different from those in Exps. 52–55; in Exp. 58 it was distinctly higher and agreed well with the rates observed in Exps. 48–51 (Table I). It is apparent therefore that starvation was not the cause of the lower respiration rate, or that, if starvation was the causative factor, one day's feeding in a rich suspension of food was insufficient for recovery.

It might be suggested that the lower rate of respiration was due to a size difference in the copepods, but it is unlikely that the animals caught on 10 September were for any reason smaller than those caught at other times. In the first place they were caught in the same locality, and, in the absence of currents passing through the area, there is no reason to expect that they came from a population different from those caught on 9 September. Secondly, the two species of *Centropages* were always separated initially by the naked eye without difficulty, since the greater size of *C. typicus* clearly distinguished it from *C. hamatus*. It is shown later that the respiratory rate is roughly proportional to the square of the length. If the observed difference in the rate of the two groups of *C. typicus* were due to size, those copepods caught on 10 September should have had a mean length of *c.* 1 mm., as compared with a mean length of 1·25 mm. for those caught on 9 September. But *C. typicus* of mean size 1 mm. would be no different in size from *C. hamatus*, and the normal separation of the two species on 10 September without microscopical examination would have been impossible.

It is clear that the two groups of *C. typicus* did not differ appreciably in mean length, and it is more likely that marked differences in respiratory rate are in some way correlated with the handling and retention of the copepods in the laboratory. It may be suggested, and support for this suggestion will be given in a later section, that the lower rate of respiration is the more correct one and that *Centropages* takęs longer to regain its normal respiratory rate after the excitement of capture and handling than does *Calanus* for which 24 hr. appears to be sufficient.

These differences in the respiratory rates of *Centropages typicus* adult females necessitated a careful scrutiny of the earlier observations in order to see whether such differences could be detected in any other species. Only one result was clearly anomalous, namely Exp. 7 with *Calanus* females (27 September) where the respiratory rate was 0·36 μl./cop./hr. as compared with a mean for the other four experiments on adult females (Exps. 8–11) of 0·86 μl./cop./hr. Again the animals used in Exps. 7 had been kept for more than 24 hr. before the measure-

ments were made. On the other hand, all the experiments done with Stage V *Calanus* from 28 August up to and including 1 September were done with animals taken from an unusually good townetting taken on 27 August, and no significant decline of the respiration rate is detectable in this group (cf. Table I, col. 5, Exps. 22–35). It may be incorrect, however, to compare Stage V *Calanus* with adult copepods. Stage V copepodites may be better able to maintain a constant metabolic rate under conditions of stress, for it must be remembered that Stage V copepodites obtained in late summer were part of an overwintering stock (cf. Marshall *et al.* 1934) which pass into deep water and possibly live at a lowered metabolic level (cf. Gross & Raymont, 1942).

TABLE III. LENGTH MEASUREMENTS

Species and stage (no. of observations)	Total length		Cephalothorax	
	Mean	σ	Mean	σ
Euchaeta norvegica:				
Female (2)	7·45	0·038	5·10	0·0
Male (8)	6·14	0·259	4·36	0·184
Stage V (5)	5·75	0·148	4·15	0·121
Calanus finmarchicus:				
Female (19)	3·12	0·118	2·45	0·091
Stage V (19)	2·66	0·225	2·06	0·175
Stage IV (31)	2·03	0·138	1·63	0·226
Centropages typicus:				
Female (37)	1·86	0·111	1·25	0·095
Male (8)	1·74	0·089	1·21	0·040
Stage V (2)	1·66	0·186	1·21	0·074
Stage IV (1)	1·32	—	0·95	—
Centropages hamatus:				
Female (10)	1·47	0·096	1·06	0·097
Male (8)	1·29	0·089	0·94	0·076
Stage V (1)	1·16	—	0·79	—

Table III gives the mean lengths of the groups of copepods measured. Two measurements are given for each group: (1) the length of the cephalosome and metasome, i.e. the 'cephalothorax'; and (2) the total length including the urosome. The advantages of measurements of the 'cephalothorax' are threefold: it is the bodily dimension that is easiest to measure accurately; it is the dimension most commonly used in measuring copepods; and thirdly, if the respiration rate is to be related to any power of a linear dimension, it will be more closely associated with some power of the length of the cephalothorax than with a power of the total length, since the cephalothorax makes up by far the greater part of the bulk of the animal. Our measurements agree reasonably well with previous measurements of copepods in the Clyde area (Marshall 1933, 1949; Nicholls, 1934).

DISCUSSION

The measurements made of the respiratory rate of *Calanus finmarchicus* agree well with those determined previously by Marshall *et al.* (1935), and by Clarke & Bonnet (1939). On both previous occasions measurements were

given in ml./1000 cops./hr.; these are numerically the same when expressed in μl./cop./hr. Marshall *et al.* made no observations at 17° C., but their curve for the relationship between temperature and respiratory rate gives a value of 0·44 μl./cop./hr. for *Calanus* Stage V, which does not differ significantly from the mean value of our measurements, 0·52 μl./cop./hr. ($d/\sigma_d = 1{\cdot}05$). Clarke & Bonnet's experiments at 16·8° C. give a rather higher respiration rate, (0·80 μl./cop./hr.), the difference from that given by the present observation being statistically significant ($d/\sigma_d = 3{\cdot}4$). However, the order of magnitude is the same, and in the present poor state of knowledge of the physiology of plankton, the agreement can be regarded as reasonably satisfactory. The respiration rates for male and female *Calanus* found by us were both higher than those given by Marshall *et al.*, that for females (0·86 as compared with 0·66 μl./cop./hr.) being significantly so, but again the agreement is reasonably good.[1]

Zeuthen (1947) quotes one measurement of the respiration of *Centropages hamatus*, giving a mean respiration rate of 0·08 μl./cop./hr. at 16° C. This agrees fairly well with the measurements here recorded which have a mean of 0·11 μl./cop./hr. This agreement too becomes even closer when account is taken of the size of the animals: Zeuthen's copepod was 0·86 mm. long (presumably total length) compared with the mean total length of 1·30 mm. for the *C. hamatus* given here.

Marshall *et al.* (1935) found marked falling off in respiration with time after capture, especially between the time of capture and 24 hr. later. Clarke & Bonnet (1939) found no such decline but their results are hardly comparable, as they did not use animals until the day after capture—the practice followed in the experiments reported here. Zeuthen (1947), citing a single measurement of the respiratory rate of *C. hamatus*, found a decline during the course of his experiment. In the present series of observations, there was no very obvious decline during the course of individual experiments. However, if the mean oxygen consumption is calculated at the end of each 30 min. period for the experiments with *Calanus* Stage V, the rate of consumption appears to fall (Fig. 1), since the points for times shorter than the mean time (1·75 hr.) lie above and two of those for longer times lie below the straight line drawn from the origin through the means (1·75 hr. and 11·38 μl. O_2 consumed). But closer examination shows that only one of the means differs from the corresponding point on the straight line by as much as its standard error, and the deviation of this one, that for the second group, is less than three times its standard error so that the differences are insignificant. It is therefore improbable that there was any real falling off in the respiration rate during our experiments.

[1] Comparison is made more difficult by the fact that the curve drawn by Marshall *et al.* showing the relationship between temperature and respiratory rate appears to be based on a single experiment, while different respiratory rates are given for other experiments at a given temperature. Thus the respiratory rates of female *Calanus* at 15° C. is given on p. 8 as 0·57, on p. 12 as about 0·70 (for normally saturated sea water), while on p. 15 a value of 0·74 is given for a temperature of only 12° C.

It is generally true that the respiratory rate of animals is related approximately to their surface area. Hence, since the copepods used in the experiments described above are all closely comparable in shape, some relationship may

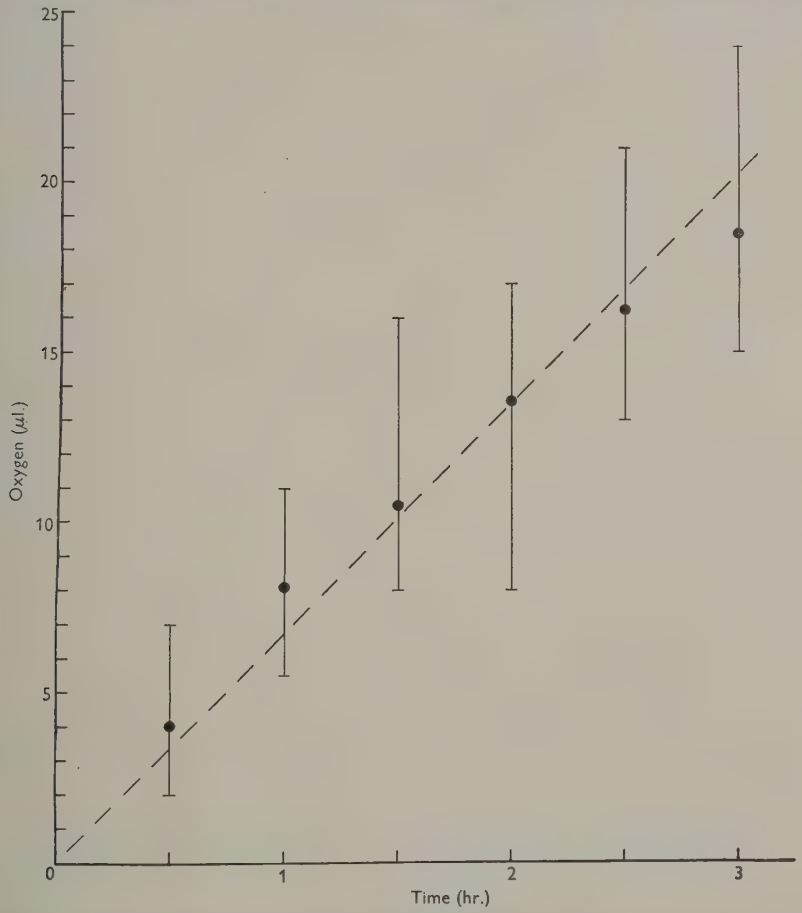

Fig. 1. Oxygen consumption by ten copepods at half-hourly intervals after start of an experiment.

be expected between their respiratory rate and the square, or some power close to the square, of their length. In Fig. 2 the respiratory rate is plotted against the length, on logarithmic co-ordinates, and it can be seen at once that the observed values lie very nearly on a straight line. The calculated regression line of the logarithm of the respiratory rate (R) on the logarithm of the length (L) is

$$\log R = 2{\cdot}193 \log L - 0{\cdot}9278,$$

from which it can be seen that in these measurements the respiratory rate was related to the length to the power of 2·19.

Zeuthen (1947, p. 81), in his analysis of the relationship between respiratory rate and body size, found that this relationship could be most satisfactorily expressed as the 'percentage decrease in metabolic rate at ten times magnification of the animal'. He expressed metabolic rate in terms of oxygen consumed

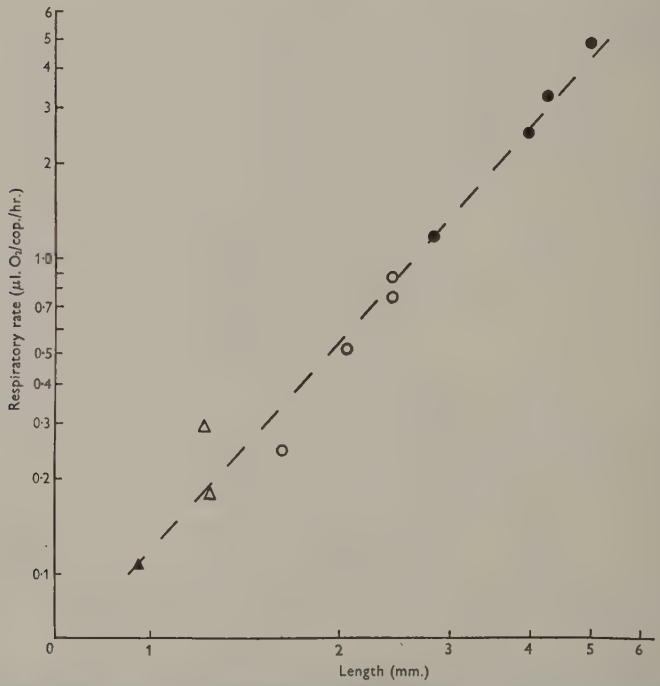

Fig. 2. The relation between respiratory rate and size of different copepods, plotted on a double logarithmic scale. (Respiratory rate in µl. O_2 per copepod per hour; length in mm.) ○, *Euchaeta norvegica*; △, *Centropages typicus*; ●, *Calanus finmarchicus*; ▲, *Centropages hamatus*. The pecked line is the regression line, given by

$$\log R = 2{\cdot}19 \log L - 0{\cdot}928.$$

per unit nitrogen content $\left(\frac{\mu\text{l. } O_2 \times 10^{-2}/\text{hr}}{\gamma N}\right)$ or per unit of weight, and showed that for a ten times magnification of the body size, the percentage decrease declined fairly steadily from *c.* 52 % for medium-sized animals (10 g.–1000 g. wt.) to only *c.* 20 % for small copepods. The percentage decrease for animals of the size range used in this present investigation he found to be

30–40 %. In the experiments described here no measurements of weights or nitrogen contents were made, but weight is usually closely proportional to the cube of the length for animals of similar shape so that a rough comparison with Zeuthen's results can be made by expressing metabolic rate as rate of oxygen consumption divided by the cube of the length.

In the measurements made above there are three pairs of figures from which percentage decrease in the metabolic rate for a ten-times magnification of size can be calculated. *Euchaeta* females are very nearly ten times the size (as given by the cube of the length) of *Calanus* females, *Euchaeta* males are just less than ten times the size of *Calanus* Stage V and *Calanus* Stage V are nearly ten times the size of *Centropages hamatus*. The decreases in metabolic rate (expressed by respiratory rate divided by the length cubed) found for these pairs are 30, 35·75 and 49·75 % respectively, with a mean of 38·5 %. The decrease in metabolic rate for a ten times increase in size calculated from the regression of respiratory rate on length given above is 46 %. These figures agree very well with Zeuthen's figure of 30–40 % for animals of the range of size represented by the copepods used in the present experiment.

The difference between the respiratory rates of the two groups of experiments with *C. typicus* has been discussed above. The distribution of the observed points given in Fig. 2 suggests that the lower value might be the more correct one, or at least that corresponding to the figures found for the other species. The deviation of the higher value (0·29 μl. O_2/cop./hr.) from the regression line

$$\log R = 2{\cdot}193 \log L - 0{\cdot}9278$$

is 0·19, twice the standard error of estimate (0·09), whereas that for the lower value (0·18 μl. O_2/cop./hr.) is only 0·03. The agreement of the lower rather than the higher respiratory rate for *C. typicus* with those for the other species is made even clearer by calculating a regression omitting the higher value. This makes a slight but not clearly significant improvement in the correlation coefficient and gives regression equation

$$\log R = 2{\cdot}302 \log L - 0{\cdot}9901.$$

The deviation of the higher respiratory rate from this line is more than three times the standard error of estimate, i.e. this value almost certainly differs from the group of values represented by this regression line, while the deviation of the lower value is less than half the standard error of estimate.

Several suggestions could be made to account for an enhanced respiratory rate in *Centropages* as found in Exps. 48–51 and 58—for instance, that *C. typicus* is excited more easily than other species by handling or by light, but in the absence of any information about the factors which might have produced the increase of the respiratory rate, further discussion is not profitable.

The question as to which of the two respiratory rates found for *C. typicus*

represent the 'true' value leads to the wider question, namely how far the rates as determined for the other species (*Calanus*, *Euchaeta*, *Centropages hamatus*) are true for these copepods living under natural conditions in the sea. Any future discussion of nutritional requirements based on respiratory rates (cf. Pütter, 1909) must imply that the metabolic rates determined in the laboratory are true for the copepods under natural conditions. The curve given by Marshall *et al.* (1935) for respiration and temperature would permit us to calculate approximately the respiration rates for the various temperatures at which the different species are living over the seasons of the year. But there are many other factors apart from temperature that might also affect respiration. Of these some attention has been given to such internal factors as sex and developmental stage. As regards environmental conditions, there are indications that light has little effect on Stage V *Calanus* (cf. also Marshall *et al.*), though no experiments were made using bright sunlight. However, the precise effects of light as well as of such factors as feeding, season, etc., must await further study.

There remains the very pertinent question as to how far the experimental conditions in a closed respirometer may modify the metabolic rate. The experiments on *Calanus* by Marshall *et al.* seemed to show that lowered O_2 tension had little or no effect unless the concentration fell below about 3 ml. O_2/l.—a value which would never even be approached in our 3-hourly experiments. There is also the possible disturbing effect on metabolism of handling the animals. This would appear to be slight (with the possible exception of *Centropages typicus*) in view of the fact that no clear reduction in respiratory rate with time was observed in our experiments, and also since our results (for *Calanus*) agree very well with those of Marshall *et al.* who employed the Winkler technique where animals were left undisturbed for relatively much longer periods of time. From the results of a few experiments with Stage V *Calanus* (Table I, Exps. 40–42) where shaking was limited to a few minutes immediately prior to final reading of the manometers, it is apparent that shaking depressed the respiratory rate of the copepods. But no permanent injury appears to have been caused by it, since the great bulk of our experimental copepods were active and healthy after being in the respirometers, and indeed, if used for a second experiment, gave a result usually showing good agreement with the original determination. The shaking of the respirometers may have reduced respiration by interfering with the physical activity of the copepods in the respirometer flask rather than by injury of the animal.

It is obvious, of course, that we were measuring the respiratory rates of the copepods in a state of activity, but how far their activity in the respirometer corresponds to their normal activity in the sea is not easy to determine. In these measurements, as in those of Marshall *et al.* and Clarke & Bonnet, the copepods were enclosed in a very small volume of water, of the order of 1 ml. per copepod, while in the sea the water in which the copepod is swimming is

effectively infinite and its distance from its nearest neighbour is probably of the order of ten or possibly a hundred times as great as it is in the respirometer. In consequence the probability of contact with the walls of the respirometer or with other copepods is very much greater than it is in nature. This repeated stimulus of contact may keep the copepods in a comparatively excited condition and this may produce a rise in the respiratory rate.

Summary

The respiratory rates of four species of planktonic copepods were measured. In two of the species measurements were made with two copepodite stages, and with adult male and female specimens.

The rate for *Calanus finmarchicus* Stage V at 17° C. was found to be 0·52 μl./cop./hr., a figure which agreed with previous measurements.

For all the species and stages studied the respiratory rate was found to be closely proportional to the length to the power of 2·2.

The relevance of such measurements to conditions in the sea is briefly discussed.

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THE GRAZING RATE OF PLANKTONIC COPEPODS

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(Text-figs. 1–4)

Introduction

The source of the food of planktonic animals has been frequently discussed since, on the basis of his calculations of food requirements, Pütter proposed in 1907 that the particulate food available to them was quite inadequate for their needs and that they must therefore derive the greater part of their nourishment from organic substances dissolved in the water. Critical study of Pütter's experiments showed that they were unreliable, and his calculations were made generally invalid by the publication in 1908–11 of Lohmann's work on the nanoplankton in sea water. In these studies Lohmann drew attention to the existence in the sea of enormous numbers of organisms, mainly unicellular algae, from 1 to 25 μ in diameter and length, and too small to be captured by plankton nets. He was also able to show that the Appendicularia obtained their food from these minute organisms and were able to filter in an hour a volume of water many thousand times their own size. Pütter tried to show that even here the amount of plankton filtered was inadequate. Krogh (1931) pointed out that Pütter based his calculations on the numbers of organisms found in the filters, and overlooked the fact that the contents would be emptied into the gut at regular intervals, and he commented (p. 415): 'It must however be admitted that Lohmann on his side did not prove the sufficiency of the nanoplankton food for the Appendicularia.'

Pütter (1909, 1925) included Copepoda among the animals which would be unable to obtain enough particulate food from sea water. As Krogh (1931) remarked, the existence in these animals, as in others, of a well-developed gut and a complex apparatus adapted to the acquisition of particulate material is itself evidence that the bulk of their food is particulate, and examination of the contents of the gut shows the presence of particulate food (Dakin, 1908; Esterly, 1916; Lebour, 1922; Marshall, 1924). Even Pütter himself mentions 'eine grüne Masse' which was undoubtedly made up of nanoplankton flagellates. But no attempt was made to find out whether the copepods could obtain a sufficiently large quantity of food by collecting the minute organisms present in the water until 1936, when Fuller & Clarke measured the filtering rate of *Calanus finmarchicus*.

The amount of food which a filter-feeding animal can obtain in a given time is determined by the volume of water which it can filter in that time, the concentration of suitable food particles in the water, and the efficiency of the filtering mechanism. The filtering rate, i.e. the rate at which water is passed through the food-catching apparatus, is independent of the concentration of the food particles, but is dependent, like any other biological process, on the physical and chemical conditions of the environment and on the activity of the animal. For example, filtering may be discontinuous and in consequence the filtering rate during active feeding may be considerably greater than that indicated by measurements made over longer periods which include periods of inactivity. The efficiency of the filtering apparatus will depend on the size of the particles, being greatest for those which are neither so small that they are able to pass through the apertures of the filter, nor so large that they obstruct the filtering apparatus. It is possible, however, that, even with particles of uniform size, the efficiency of the filter may be variable, and may be under some kind of control by the animal.

The measurements of Fuller & Clarke (1936) and those of Fuller (1937) seemed to show that the animal's power of catching particulate food was quite inadequate for its needs. Fuller & Clarke found that *Calanus*, a large copepod, could sweep clear of carmine particles 4·5 ml. of water per day. At the same time they estimated that in order to supply its needs it would have to sweep clear about 72 ml. of water containing a rich natural diatom population. In 1937, estimating the food requirements on a different basis, Fuller stated that even with the maximum rates of filtering in his experiments (2·88 ml. per day) *Calanus* would have obtained, in water where it is known to thrive, less than one-tenth of the required amount of its food from particulate matter. On the other hand, Harvey (1937) reports a small number of experiments in which he found far more rapid filtering rates for *Calanus*, 2–4 ml. swept clear per hour with *Lauderia borealis*, a medium-sized diatom, and 7–10 ml. per hr. with the larger *Ditylium brightwelli*.

In his measurements of filtering rates, Fuller (1937) found no correlation between the concentration of food and the filtering rate, and concluded that *Calanus* obtained its food by filtering particles from a stream of water passed through the setae of the posterior cephalic appendages, and made his investigation on this assumption. However, Lowndes (1935), basing his views on anatomical grounds and on the fact that crustacean remains have been reported from the gut, states (p. 702) 'It is difficult to see any justification for describing the feeding of *Calanus finmarchicus* as being either automatic or non-selective', and implies that the bulk of its food is obtained by seizing and chewing up larger particles, especially other crustaceans.

The experiments which are to be described below throw some light on the question of filter-feeding by copepods and of the magnitudes of the filtration rate.

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Material and Methods

The experiments to be described fall into three groups; (i) those done in the Department of Zoology, Edinburgh University (Series A and D); (ii) those done in the Oceanographic Institute, Göteborg (Series B and C); and (iii) those done at the Marine Station, Millport (Series E–G). On arrival at the laboratory the copepods were sorted and transferred to cooled sterile sea water in 'breffit' jars, and at Edinburgh and Göteborg kept in a refrigerator the upper temperature limit of which was set at 10° C. At Millport the jars in which the copepods had been placed were kept in running water to cool them. Some preliminary experiments were done with the diatom *Skeletonema costatum* as food. In these experiments the diatoms occasionally settled to the bottom of the dish during the experiments, especially in experiments done in darkness. In consequence these experiments had to be abandoned, and the *Skeletonema* culture was replaced by one of a species of *Chlamydomonas*. *Chlamydomonas* is an actively motile flagellate; its approximate dimensions are: length 9·5–13·8 μ, diameter 6–8·4 μ (Raymont & Gross, 1942) and no evidence was ever seen of its settling or being unevenly distributed in any way.

For the experiments a culture of *Chlamydomonas* was diluted with sterile sea water, and divided among a number of beakers or large crystallizing dishes, each one receiving 100 or 150 ml. of this experimental medium. In some of the jars one or more, according to their size, healthy active copepods were placed; others were kept as controls. The concentration of the suspension of the food organism was estimated at the beginning of the experimental period, usually about 24 hr., and again at the end. Usually at the end of one experiment the copepods were transferred into a second set of vessels and a new experiment started.

In the first two series of experiments (A and D) the concentration of the culture of the food organism was measured by its extinction of light in a 'Unicam' photometer. This method was satisfactory only if the concentration of the food organism was rather high—very much higher than likely to occur in nature.

There was a possibility therefore that the behaviour of the copepods might be abnormal in such conditions, so that this method was later abandoned in favour of counting. In all the other experiments the concentrations were measured by counting the *Chlamydomonas* cells on a Fuchs-Rosenthal counting slide—four millimetre squares from each of five drops, making a total of four microlitres, were counted from each experimental vessel. The agreement between the counts of different drops and between the counts of different squares from the same drop was generally good.

If it is assumed that a copepod is a filter-feeding animal, then in an experimental vessel where the physical and chemical conditions are kept constant, the concentration of food particles in the presence of a steadily grazing copepod will decline exponentially, and at any given time it is given by the expression

$$C_t = C_0 e^{-kt}, \qquad (1)$$

where C_t is the concentration after time t, and C_0 the initial concentration.

Further if v is the volume of water per animal, then vk is the volume of water swept free by one animal in unit time, so that the filtering rate (F) is given by

$$F = vk. \qquad (2)$$

This expression can be evaluated from (1) in the form

$$F = v \frac{\log_{10} C_0 - \log_{10} C_t}{t \log_{10} e}. \qquad (3)$$

The results of the experiments to be described were evaluated from this formula (3) and expressed as millilitres of water swept clear by one copepod in the period covered by the experiment, usually 18 or 24 hr.

Experiments

A summary of the experiments and their results is given in Table I, and Figs. 1–3 show the results in greater detail. In the figures, the volume swept clear is plotted against the concentration of the control cultures.

Fig. 1 gives the results of the experiments done with *Pseudocalanus*. The results of experiments with *Temora* and *Centropages* are given in Fig. 2 and those with *Calanus* in Fig. 3.

Of the experiments with *Calanus* Stage V (Series E), and Stage IV (Series F), most were done over 18 hr., starting at about 16.00 hr. and finishing about 10.00 hr. the following day, i.e. the experimental period included the hours of darkness. But in Series E six experiments were continued for 24 hr. and eight for only 12 hr. The means of these two groups were respectively 82·31 and 73·62 ml. swept clear, in comparison with 69·66 ml. swept clear for the

TABLE I

Series	No. of experiments in series	Species	No. of copepods per vessel	Volume of vessel (ml.)	Duration (hr.)	Temperature (° C.)	Mean volume swept clear per copepod (ml.)	Standard deviation σ
A	21	*Pseudocalanus minutus*	1	10	24	10	4·28	1·46
B	45	*Temora longicornis*	10	150	24	10	8·38	1·91
C	8	*Centropages hamatus*	10	150	24	10	12·99	1·20
D	19	*Calanus finmarchicus* stage V	1	100	24	12·5	64·36	11·63
E	77	*C. finmarchicus* stage V	1	100	18	17	71·03	13·17
F	25	*C. finmarchicus* stage IV	2	100	18	17	36·65	8·75
G	13	*C. finmarchicus* stage III	3	100	18	17	22·24	5·58

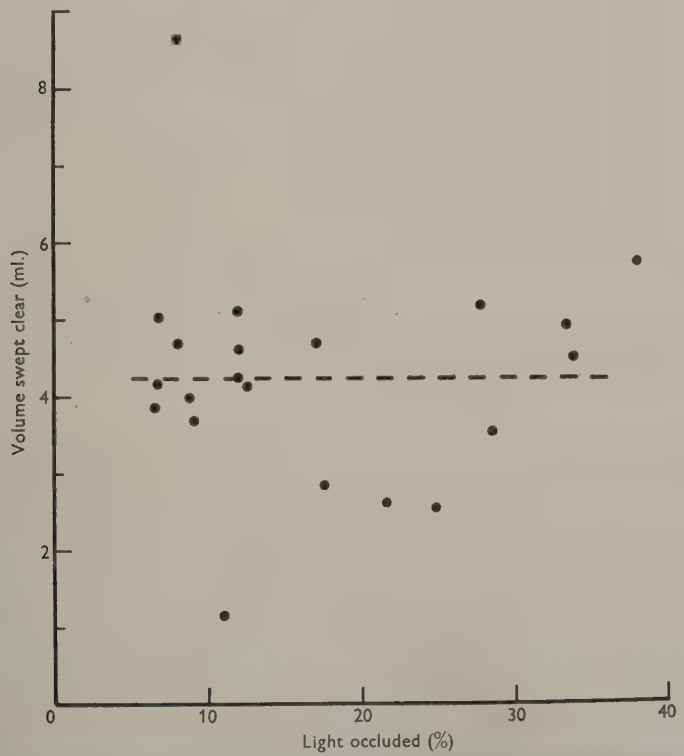

Fig. 1. *Pseudocalanus minutus*. Volume (ml.) of culture swept clear compared with the concentration of the control culture, measured by the percentage of light occluded.

remainder measured over 18 hr. The difference between the volumes swept clear in 12 and 18 hr. is not significant. The increased volume swept clear in 24 hr. is possibly significant, but only just so ($D/\sigma_m = 2{\cdot}1$).

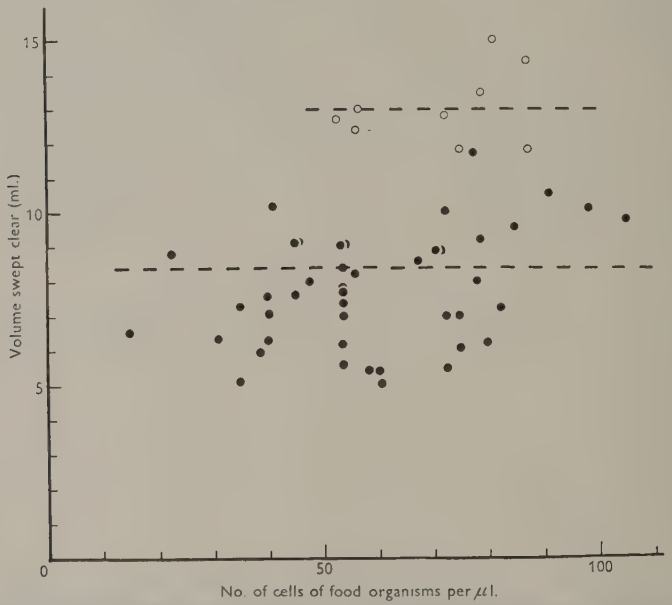

Fig. 2. *Centropages hamatus* (open circles) and *Temora longicornis* (black circles). Volume (ml.) of culture swept clear compared with the concentration of the control culture, measured as cells per μl.

Discussion

It is immediately obvious from the scatter of the points in the diagrams that in these experiments the animals were acting as filter-feeders. If they had been collecting a fixed quantity of food, the scatter of the points would have shown some trend from the upper left-hand side of the figure to the lower right-hand side: no such trend appears. On the contrary, the number of *Chlamydomonas* cells consumed by *Calanus* Stage V (Series E), for example, ranges from a minimum of about 250,000 to a maximum of 2,000,000, i.e. the largest amount consumed was eight times the smallest. On the other hand, the largest volume swept clear, 101 ml., is less than three times the smallest, 42 ml. That the volume filtered is independent of the concentration of the food particles is shown more clearly in Fig. 4 where, from the data of Series C, the difference in the concentration produced by one *Temora* in 24 hr. is plotted against the

concentration of the initial cultures. Here there is a very clear trend from lower left-hand side to the upper right-hand side of the figure, and the broken line in the figure is the graph of the difference produced by a steady filtration rate of 8·38 ml. in 24 hr., the mean of the observed rates. Similar figures could be drawn for the other series of experiments. These findings are therefore in agreement with Fuller's that there is no correlation between the concentration of the food particles and the filtering rate.

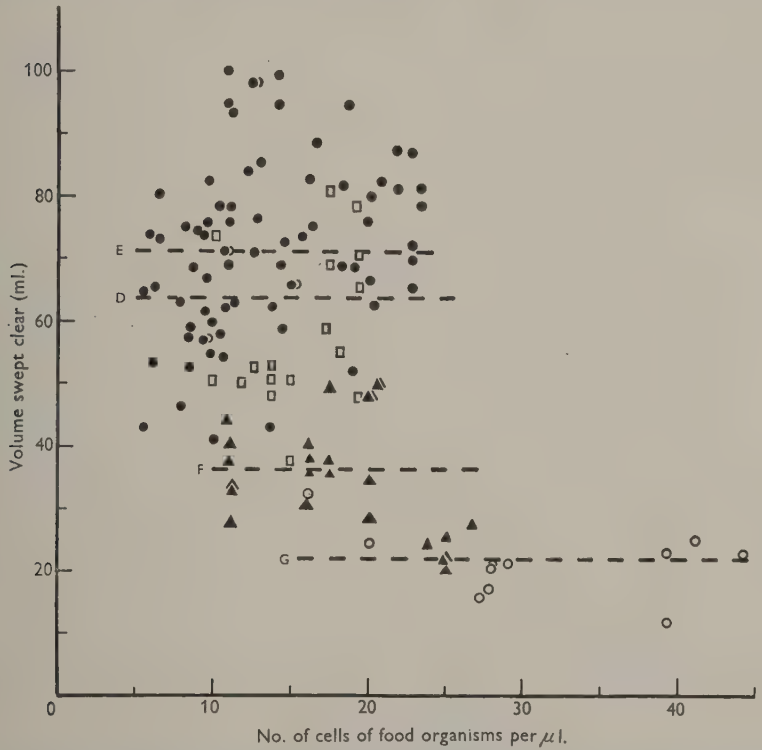

Fig. 3. *Calanus finmarchicus*. Volume (ml.) of cultures swept clear compared with the concentration of the control culture, measured as cells per μl. □, Series D, Stage V; ●, Series E, Stage V; ▲, Series F, Stage IV; ○, Series G, Stage III.

It may be objected that, while these figures (like Fuller's) show that the animals collected all the food from a given volume of water, they do not prove that it was collected by filtration although they make it more likely. However, the total number of particles consumed can readily be calculated and those for *Calanus* Stage V have already been mentioned. If it is assumed that the copepods worked continuously for the whole period of the experiment, although

it has been suggested that this may not be so, it is possible to calculate how many particles were collected in unit time. In the experiments with *Calanus* Stage V (Series E) this works out at nearly 4 per sec. from the lowest figure to over 30 per sec. from the highest. Similar collecting rates apply to the other experiments; *Temora*, for instance, collected particles at a rate of from 1½ to 9

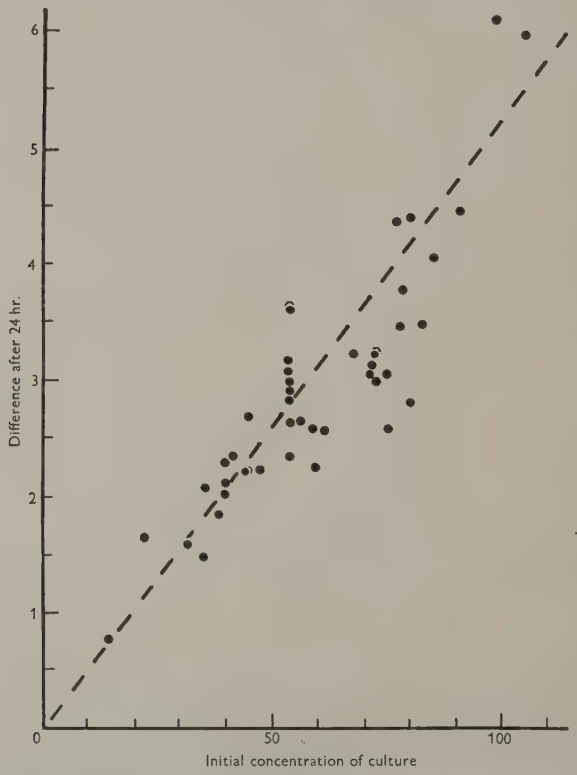

Fig. 4. *Temora longicornis*. Difference in the concentration of food organisms produced by one copepod in 24 hr. plotted against the concentration of the initial culture. Units are cells per μl.

particles per sec. in the experiments in Series C. It is difficult to imagine any way in which the animals could collect particles so rapidly except by filtration, especially since it is probable that the copepods fed actively during a part only of the experimental period and so must have collected their food even more rapidly than the figures show.

The magnitude of the filtering rates found here for *Calanus* is much greater than those found by Fuller & Clarke (1936) and Fuller (1937). The 1936 measurements were made by estimating the rate at which carmine particles were removed from the water. Some of the carmine was definitely ingested but it is possible that the bulk was rejected after it had been collected on the filtering apparatus and that the apparently low filtering rates were due to return to the water of the particles so rejected. Fuller (1937) measured the filtering rate by estimating the change in the concentration of cultures of the diatom *Nitzschia closterium* (Plymouth strain), and found rather smaller filtering rates than Fuller & Clarke. *A priori*, *Nitzschia* might appear to be suitable for such measurements since *Calanus* has been reared on cultures of this diatom (Crawshay, 1915), but the experiments of Harvey (1937) seem to show that for some reason it is unsuitable, since he found very low filtering rates with *Nitzschia* although with other diatoms, *Ditylium* and *Lauderia*, he obtained very much higher rates. One criticism may be made of Fuller's experiments. The measurements were made in vessels in which three copepods were confined in 15 ml. of water. In view of the size and activity of *Calanus* this seems to be a very small amount of water for each animal, and indeed it is difficult to see how volumes swept clear much larger than 5 ml. per animal could be measured in such experiments.

The measurements of Harvey (1937) are of the same order of magnitude as those recorded here for *Calanus*, but immediate comparison cannot be made because his experiments covered variable and rather short periods and the results are given as filtering rates per hour. If it is true that *Calanus* filters intermittently, results based on short periods of observation are liable to be misleading, since an experiment which covers a period of a few hours may or may not include part of a period of active filtration. Two of Harvey's experiments however covered a 24 hr. period and the volumes swept clear in these were 74 and 94 ml. per *Calanus*. One experiment of 48 hr. showed a total filtration of 96 ml. per copepod, and of the measurements made over periods of less than 24 hr. none exceeded 70 ml. These results therefore do not contradict the hypothesis that *Calanus* filters a volume of about 70 ml. per 24 hr., but that the greater part of this filtration is confined to a relatively short period.

Riley, Stommel & Bumpus (1949) calculated the filtering rates of mixed plankton populations, and found filtering rates of 80–110 ml. swept clear per day for each milligram (wet weight) of zooplankton. Bogorov (1934) gives the wet weight of *Calanus* Stage V as varying between 0·35 and 0·70 mg. with a mean value of 0·53 mg. From these figures the filtering rate of *Calanus* Stage V can be calculated, giving an overall range of from 28 to 77 ml. swept clear per day, values which agree very well with those found in the present experiments, in spite of the roundabout way in which they have been reached.

Fuller (1937) found that the diatom concentration in his experimental vessels often remained stationary for a day or more, showing that feeding was

not a continuous process, and in some of his experiments he reported a diurnal feeding rhythm in which the diatoms were removed more rapidly at night. Such a rhythm is suggested by the observation in the present experiments that there is little difference between the amount of grazing in 12, 18 or 24 hr., but sufficient evidence is not available to show the period, or periods, during which grazing was most active, or the causes of the rhythm.

Comparison of the filtering rates found for the different species and stages is difficult because the experiments were carried out at different temperatures. If, however, it is assumed that the relation between temperature and filtration rates is the same as that between temperature and respiratory rate, and the observed rates are all corrected for a single temperature (10° C.), it can be shown that the filtering rates are approximately related to the squares of linear dimensions. (The correlation coefficient between the filtration rate and the square of the length is 0·84.) However, the range of size covered by these experiments is small and the variation in the observed values of the filtering rates rather large, so that more detailed mathematical investigation of this relation is not justified without further evidence.

In discussing Harvey's results, Fuller (1937) suggested that *Calanus* was better able to retain large particles on its filtering surface than small ones, and that the low filtering rates found by Harvey and himself with *Nitzschia* were due to the small cells of *Nitzschia* passing through the filter. But Harvey's observation (Exp. C, p. 98) that, in a mixed suspension of *Lauderia borealis* and a species of *Chaetoceros*, *Calanus* reduced the concentration of *Lauderia* from 13 to 1·9 per ml. in 48 hr. 'without any considerable reduction in the *Chaetoceros* population', cannot be explained in this way. The species of *Chaetoceros* used in this experiment was almost certainly larger than *Nitzschia closterium* forma *minutissima*, which Harvey found to be removed in appreciable amounts, though much more slowly than *Lauderia* in Exp. N 90. Wilson (1946) states that this form of *Nitzschia* is 3–4 μ in diameter and 25–35 μ in length. It is impossible to be certain of the size of the *Chaetoceros* species used, but none of the measurements given in Lebour (1930) for any species of *Chaetoceros* is less than 4 μ broad. In addition, *Nitzschia closterium* is a solitary species while the species of *Chaetoceros* nearly all form chains and the spines characteristic of the latter genus might increase the effective diameter of a chain of cells, possibly to five times that of the cells. Riley *et al.* (1949) suggested that the result of Harvey's experiment was due to the rejection by *Calanus* of *Chaetoceros* 'which in chains would presumably be larger than *Ditylium*' (p. 64), and implied that *Chaetoceros* in chains was too large to be eaten by *Calanus*. This is not so since *Calanus* is known to feed on *Chaetoceros* (Marshall, 1924; Raymont & Gross, 1942). That chains of *Chaetoceros* cells may be larger than a *Ditylium* cell is probably unimportant since diatom chains are readily broken up, much more so than the cells of *Ditylium* which *Calanus* cannot swallow whole but has to break up, as it does many large diatoms

(Marshall, 1924). If the size of the particles were the only factor in the selection of food by copepods as Fuller and Riley *et al.* suggest, Harvey's grazing rates suggest that the optimum size of particle is one about the size of a *Ditylium* cell or a *Lauderia* chain which would be about the same size and shape, approximately a cylinder 40–50 μ in diameter and 100–200 μ long. *Chlamydomonas*, the food organism used in the experiments described in the present paper, is a solitary flagellate, entirely without projections of any kind, and its linear dimensions are nearly ten times smaller than *Ditylum* and of the same order as those of *Nitzschia*. Raymont & Gross (1942) give its dimensions as 6–8·4 μ by 9·5–13·8 μ, and a small number of measurements made recently agree closely with those. Yet in the experiments described here *Calanus* filtered the *Chlamydomonas* at the same rate as Harvey found with *Lauderia*, and nearly twenty times as fast as it filtered *Nitzschia*. It is clear that selection is not merely a matter of size, and some more active mechanism of selection may be involved, but sufficient evidence is not available for further discussion to be profitable.

Fuller & Clarke (1936) and Fuller (1937) attempted to relate the filtering capacity of *Calanus* to its food requirements. Fuller & Clarke computed the volume an individual *Calanus* would require to filter in Vineyard Sound in July in order to obtain its minimum food requirements as 72 ml. per day. From a different estimate of the available food, Fuller calculated that a single *Calanus* would need a minimum filtering rate of the order of 30 ml. per day. If this latter estimate is correct, the filtering rate found in the present experiments is quite adequate. But since the amount of food provided by the phytoplankton at any time and place is still uncertain, and the daily requirements of a copepod are difficult to assess, further attempts to relate filtering rate and food requirements can have little value until more evidence is available.

Summary

The filtering rate of four species of marine planktonic copepods was measured by estimating the rate at which they consumed cultures of *Chlamydomonas*.

The filtering rate was independent of the concentration of the food organism and it is concluded that the copepods were acting as filter feeders.

The filtering rates were much greater than those reported by Fuller & Clarke (1936) and Fuller (1937), but agreed with those reported by Harvey (1937).

Some evidence was obtained that grazing was restricted to some only of the 24 hr., most probably to the hours of darkness.

The filtering rates were approximately proportional to the square of the linear dimensions of the copepod.

The purely mechanical selection suggested by Fuller (1937) to account for differences in filtering rates obtained with different species of diatoms cannot account for all the differences which have been observed.

It is probable that the copepods could obtain sufficient particulate food in the sea by filtering a daily volume of water corresponding to the filtering rates found.

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THE STATUS OF THE COMMON SEAL (*PHOCA VITULINA* L.) ON THE EAST ANGLIAN COAST

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(Text-fig. 1)

From time to time over a number of years the Fisheries Laboratory at Lowestoft has been asked to investigate aspects of the problem of the alleged harm to fisheries caused by the common seal. There are numerous colonies of these animals off the East Anglian coast, frequenting especially the sandbanks of the Wash, which dry out at low water, and therefore form secluded resting places.

It would be a major undertaking to make a full estimate of damage done by the seals, whether this is large or small; but evidence on which a judgement can be based has been collected, and is given in the following pages. This evidence is often inconclusive, but in one locality it clearly shows harm done by the seals, and in the author's opinion it would be prudent from time to time to reduce the number of seals, incidentally finding a commercial use for the meat and hides.

The evidence comes from an investigation of the food of the seals, and of their numbers, to which are added some notes on their biology.

This work was carried out in the summer of 1947 and the spring of 1948 at the Fisheries Laboratory, Lowestoft, and grateful acknowledgement is made of help given by members of the staff of the laboratory in its progress. I am particularly indebted to the director, Mr Michael Graham, for allowing me to incorporate the results of his own earlier investigations in this paper, for reading through the manuscript and suggesting improvements, and for encouraging its publication.

I am grateful also to Dr G. C. L. Bertram, Dr F. Fraser Darling and Mr P. H. T. Hartley, for valuable criticism and advice, and to Dr Bertram for the loan of several papers otherwise unobtainable.

Finally, I am indebted to Prof. James Gray for permission to submit the paper for publication while I have been engaged on other research work under his supervision.

Food

Altogether 194 stomachs of seals obtained in the Wash district during 1947 were examined, 2 of these with the complete gut. In addition, 6 stomachs from the Blakeney district of the Norfolk coast, and 2 unpreserved stomachs from

seals killed on the Scroby Sand, off Yarmouth, were examined. The last were sent by Messrs Pettit of Reedham. All the rest were sent by the Eastern Sea Fisheries Joint Committee, while a scheme was in operation under which fishermen received a bounty for each stomach collected and preserved in formalin. These were forwarded to the Fisheries Laboratory in milk-cans for examination.

To supplement the results of these examinations a 3-day visit was made by the author in April 1948 to King's Lynn and the coast of North Norfolk as far east as Sheringham, and inquiries were made of fishermen at Lynn, Wells, Brancaster, Blakeney and Sheringham. These inquiries yielded eye-witness accounts of the feeding of seals and the stomach-contents in freshly killed seals. The author has, in addition, observed seal herds in the Wash on several occasions, and has been able to study the bottom fauna brought up by the trawls of shrimping vessels in that estuary, as an indication of the food available to the seals there.

Of the 202 stomachs examined, all came from seals killed between June and September, with the exception of the two from Scroby Sand which had been killed in March. Thus the results do not indicate a complete year's feeding habits, and more spring-killed seals would have been desirable, for example, to examine for remains of sea-trout (which appear to be caught off the Norfolk coast by the fishermen in May).

Only date and position of capture were given with the stomachs, with no information available as to the size or sex of the seals from which they had been taken. However, it was possible to distinguish the young and first-winter animals by the small size and thinness of their stomachs. All other stomachs are labelled 'adult'. Of this total of 202 stomachs, 106 were those of young seal pups, containing (if anything) only milk. Of the remaining 96, only 25 contained recognizable food remains; so that the number does not permit of a quantitative evaluation of the food eaten. However, it has been possible to confirm the results from earlier work, previously unpublished, carried out by Mr M. Graham from 1926 to 1930 on the food of seals in this region. These results are included in the tables (see Table I separately and together with the results of the present investigations.

To account for the small percentage of stomachs containing any food remains at all it is presumed that most of the seals were killed while resting on sand-banks at low water, some time after their last meal. Digestion in these animals is very rapid, all traces of food having left the stomach within 3 hr., according to Havinga (1933).

From the data available, the food of seals frequenting the Wash may be summarized as follows:

The pups are suckled for at least a month. Havinga (1933) gives 6 weeks from birth to weaning, and my results indicate about the same time—all pups were feeding on milk up to 10 July, and some were still unweaned by the 25th.

However, some began to feed on shrimps about 12 July onwards, and these became the predominant food until about the middle of October. Havinga also found, from analyses of stomach contents, that young seals on the Dutch coast fed largely on shrimps in their first autumn.

TABLE I. SUMMARY OF FOOD FOUND IN STOMACHS OF SEALS FROM THE WASH (ADULT AND IMMATURE), 1929 AND 1947

	No. of stomachs in which found			Total number of individuals of species		
Species	Graham 1929	D.E.S. 1947	Total	Graham 1929	D.E.S. 1947	Total
Fish:						
Flatfish (*Pleuronectes* spp.)	5	2	7	*c.* 15	2	*c.* 17
Whiting (*Gadus merlangus*)	2	1	3	2	1	3
Sand eel (*Ammodytes* sp.)	1	—	1	1	—	1
Salmonid (?)	—	1	1	—	1	1
Pipefish (*Syngnathus* sp.)	—	1	1	—	15	15
Unidentified	1	1	2	1	1	2
Mollusca:						
Common whelk (*Buccinum undatum*)	17	6	23	158	14	172
Squid (*Loligo* sp.)	—	3	3	—	5	5
Mussel (*Mytilus edulis*)	—	3	3	—	8	8
Cockle (*Cardium edule*)	4	2	6	4	2	6
Crustacea:						
Common shrimp (*Crangon vulgaris*)	5	9	14	110	245	355
Prawn (*Pandalus montagui*)	1	—	1	50	—	50
Crabs (*Carcinus* or *Portunus* sp.)	—	1	1	—	1	1
Hermit crabs (*Eupagurus* spp.)	1	1	2	1	1	2
Unidentified	1	—	1	2	—	2

Totals calculated by weight at time of assimilation, including shell weight for the Mollusca: all fish 4%, Mollusca 92%, Crustacea 4%.

There is thus after weaning a transitional shrimp-eating stage. Then, in their first winter, the seals become more omnivorous and eat fish, crabs, etc., as well as shrimps. As may be seen from Table I, the food of adult seals in the Wash appears to be predominantly the Common Whelk (*Buccinum undatum* L.), the opercula of which were found alone and in some numbers in many stomachs, in both investigations. Fish are not a large item, but flatfish (*Pleuronectes* spp.), whiting (*Gadus merlangus* L.), pipefish (*Syngnathus* sp.), and salmonid remains were identified from whole remains, otoliths, or vertebrae. Other food includes squids (*Loligo*, sp.), shrimps, hermit crabs (*Eupagurus* sp.), true crabs (*Carcinus maenas* Penn. and *Portunus* sp.), and small mussels (*Mytilus*).

The sample from Blakeney shows a complete contrast. The number of stomachs was relatively small, but most were full, and showed an overwhelming preponderance of fish-remains. Reports from fishermen confirm these piscivorous tendencies. Apart from flatfish (Pleuronectids) and gobies (*Gobius*

minutus Gmelin) which were found in the stomachs sent in, soles, eels, mackerel and sea-trout are said to have been found in stomachs opened by the fishermen themselves in the past, and in addition seals have been watched feeding on skates and cod.

No food remains were found in the two intestines examined.

It is possible that the percentage of fish has been underestimated, since (i) the small fish otoliths would pass out of the stomachs more rapidly than the larger whelk opercula, etc., and (ii) the heads of fish may, according to eye-witnesses, be bitten off, and rejected, leaving only the more rapidly digested vertebral column for recognition.

Table II

A. Food Found in Stomachs of Seals from Blakeney (six Stomachs, three containing Food Remains, October–December, 1947)

Species	No. of stomachs	No. of individuals	Remarks
Dab (*Pleuronectes limanda*)			
Plaice (*P. platessa*)	3	*c.* 90	All 10–12 cm. in length
Flounder (*P. flesus*)			
Common goby (*Gobius minutus*)	2	*c.* 12	—
Unidentified elasmobranch	1	1	—
Shrimp (*Crangon*)	2	2	—
Hermit crab (*Eupagurus bernhardus*)	2	2	—
Crab (*Portunus* sp.)	1	8	—
Mussel (Mytilus)	1	1	—

B. Food Found in Stomachs of seals from Scroby Sand (two Stomachs, April 1948)

(i) 1 pleuronectid (ii) 3 shrimps (*Crangon*)

Some of the smaller invertebrates may have been taken as secondary food, i.e. that eaten by the seal's prey; but this has been considered for each individual, e.g. small worms (*Lagis* sp.) associated with flatfish were certainly the food of the latter, but crabs with a carapace width of *c.* 25 mm. in the same stomach could not have been so. The whelks must certainly have been taken directly, as they were never associated with any fish remains.

Thus the results for adult seals from the Wash contrast strongly with those from the open coast at Blakeney. Examinations of shrimpers' catches in the Wash show that shrimps form the great bulk of the free bottom fauna, while fish of any size are rare. Small flatfish of 2–3 in. in average size, small gadoids and the common goby are the principal small fish brought up in these fine-meshed trawls, together with occasional sprats (*Clupea sprattus* L.), the sea-snail (*Liparis montagui* Don.), and the armed bullhead (*Agonus cataphractus* L.). Whelks are presumably common: although the trawls do not take them, there are local fisheries for whelks at Brancaster and Wells just outside the bay of the Wash. In the Wash there are no inshore fisheries dependent on fish, as there

are on the open coast. All the boats at Lynn and Boston are used either for shrimp-trawling, or for gathering cockles (*Cardium edule* L.) or mussels from the beds in the Wash. The evidence suggests, therefore, that the common seal in this district has catholic tastes in its choice of food, fish comprising the normal or 'first-class' food, and invertebrates predominating when fish are difficult to secure. All of the animals upon which the seals feed, with the exceptions of the squids, are bottom-living. The substratum in shallow water along the coast and in the outer part of the channels of the Wash is clean sand, grading into mud, and finally into heavy estuarine clays in the river-channels of the Great Ouse, Nene, Welland and Witham.

Havinga found the seals of the Dutch coast to be feeding almost exclusively on fish, which together accounted for about 97 % by weight of the total food. The most important species, in descending order, were: flounder (*Pleuronectes flesus* L.) 30 %, whiting (*Gadus merlangus* L.) 17 %, herring (*Clupea harengus* L.) 15 %, and the bullheads (*Cottus scorpius* L. and *Agonus cataphractus* L.) together 16 %. Shrimps, eaten mainly by the young seals, made up the bulk of the remaining 3 % of invertebrate food, which also included a few cuttlefish (*Sepia officinalis* L.). Whelks were not recorded at all, and Havinga was sceptical of the earlier findings, then unpublished, which have been included in this paper. But as he used exactly the same methods of computation after analysis of stomach contents, one can only conclude that whelks are a food taken but locally. The seals on the Dutch coast, which included herds both on the open coast and in the channels of the Scheldt-Maas estuary, were thus found to have a diet resembling in a general way that of seals on the Norfolk coast, directly across the North Sea, as far as one can say from the relatively few data available from the English side. No doubt a more extensive investigation would show a more detailed correlation with the relative abundance or scarcity of individual food species in different areas and at different seasons. However, it seems strange, when one considers how much richer are the inshore waters of the Dutch coast than those of the opposite North Sea coast in young plaice, to find that this species comprised only some 3 % of the total fish-food in Havinga's investigations.

Scheffer & Sperry (1931) (and see also Scheffer & Slipp, 1944), studied the food of the subspecies *Phoca vitulina richardii* (Gray) on the Pacific north-west coast of the United States. Their results, based on analysis of eighty-one stomachs with food-remains, were as follows: fish 93·6 % by volume, mollusca 5·8 %, and Crustacea 0·6 %. The most important fish were: Pleuronectidae, various gadoids, the Pacific herring (*Clupea pallasii*), and various Cottidae, in that order; the Mollusca: squids, an octopus, and a bivalve (*Yoldia myalis*); the Crustacea: shrimps (*Crago* spp.), crabs, and the burrowing prawns *Upogebia* and *Callianassa*. These data show a striking similarity to those of Havinga (with respect to the principal families and genera, though not of course, the species, of the fish) and to the data here presented, with respect to the

available invertebrates. Thus it seems that within a wide range of available food animals certain types seem to be preferred. The most easily available of these in any one locality and at any given season will then bulk largest in the diet, and the seals may (as in the Wash) adapt themselves permanently to feeding almost exclusively on one or two of these forms.

This adaptiveness in feeding-habits agrees well with what one knows of the highly developed adaptive behaviour of the common seal in other ways, for instance its rapid learning of relative safety or danger in different circumstances. It will also mean that food is not likely to be a limiting factor in the distribution of the species.

In fact, *Phoca vitulina* on the coasts of Europe ranges from the Mediterranean and Portugal to Iceland and the White Sea (Doutt, 1942), and within the British Isles where it is widespread the range of habitats is a wide one, not apparently related to any particular type of coast. Thus, common seals are found in the sea lochs of the Western Highlands and the Hebrides, and along the exposed coasts of the Shetlands, as well as in estuaries and on sandy coasts as in the east of England and Scotland. The only general preference that can be noted is for sandy coasts, with sandbanks or low islets on which the herds can haul out at low tide.

By contrast, the grey seal (*Halichoerus grypus* F.) keeps to more remote islands and coasts, always on exposed shores. It appears to be a more specialized fish-feeder (as one might guess from comparing its sharply pointed teeth with the more lobose cusps of the common seal's), and it hunts especially the Gadidae and other inshore fish of rocky coasts (Darling, 1948, p. 222). However, it is a species which is very vulnerable at the breeding season, since the young cannot swim until some days after birth, and do not naturally enter the water for some weeks. Persecution by man has undoubtedly confined it to the more remote islands.

Of other members of the genus *Phoca*, the harp seal (*P. groenlandica* Müll.) of the Arctic feeds on pelagic crustacea and fish (Sivertsen, 1941), as does the ringed seal (*P. foetida* Müll), which was found by Dunbar (1941) to feed in the Canadian Arctic chiefly on the amphipod *Themisto libellula*.

Population

An inquiry was carried out in the spring and summer of 1948, with the help of local fishery officers of the Eastern Sea Fisheries Joint Committee, in order to find the approximate numbers of seals along the east coast from south Lincolnshire to Suffolk. Officers were asked to count the herds on sandbanks frequented by seals in their respective districts, where possible on several dates as a check. The response was good, the whole coast from Skegness to Yarmouth being covered, and the writer wishes to express his thanks to the fishery officers concerned for this information. The counts were made chiefly between

April and June, i.e. at a time when the population, prior to breeding, should be at a maximum, while as yet no young would be present to complicate the estimate.

Details of the counts, with previous counts and estimates of the total number of seals in the Wash and of the number killed in each of these years, are given in Table III. Data for years other than 1948 were taken from unpublished records in the possession of the Fisheries Department.

The accompanying map shows the approximate positions of herds located in 1948.

TABLE III. SUMMARY OF DATA ON SEAL POPULATION IN VARIOUS YEARS, FROM 1912 TO 1948

Sand	1912	1920	1924	1928	1947	1948*
Scroby Sand	—	—	—	—	—	120–140
Blakeney Point	—	—	—	—	—	*c.* 150
Burnham Overy	—	—	—	—	—	10–20
Total for open coast	—	—	—	—	—	280–310
Woolpack Middle Sand	—	—	*c.* 50	—	—	*c.* 150
Blackguard Sand	—	—	—	—	(18 killed)	40
High Soft or Seal Sand	—	—	—	—	(19 killed)	40–50
Thief Sand	—	—	—	—	(21 killed)	150
Inner Westmark Knock	—	—	—	—	250	20–30
Old South	—	—	—	—	(53 killed)	80–120
Gat Sand	—	—	—	—	(4 killed)	—
Hook Hills	—	—	—	—	—	10–14
Black Buoy Sand	—	—	—	—	(1 killed)	—
Roger Sand	20	30–40	200	—	(3 killed)	28–34
Ants	—	50	—	—	—	30
Long Sand	300	50	—	—	—	'Hundreds' 40 (Sept.)
Inner Dog's Head	350	400	300	—	—	100 (Sept.)
Inner Knock	50	100	100	—	—	30 (Sept.)
Wainfleet Mains	—	—	—	—	—	43 (Sept.)
Total for Wash	'2000'	750 counted	'Very abundant'	750–1000	—	750–850
Total killed in Wash	*c.* 100	—	150	200?	300	100

* All counts in 1948 were made between April and June unless otherwise stated.

The totals given by these counts for the year 1948 are: 750–850 for the herds in, and on the margins of, the Wash, and 300 for the herds along the Norfolk coast, giving a total of between 1050 and 1150 seals. In spite of the usual human tendency to estimate too high, this is probably an underestimate, since (i) the number counted on a sand at any time is unlikely to include all the seals in the vicinity (some being in the water may easily be missed); and (ii) a herd or two probably went unrecorded. Repeated counts over a period of some weeks at several sands showed that these herds did not fluctuate greatly in numbers, and therefore probably remained as fairly static units which did not move about to different sands to be recorded more than once. I would therefore estimate about 850 seals as the approximate population in the Wash. This is of

the order of magnitude of earlier estimates, e.g. 750 counted in 1913, and 750–1000 estimated by Mr Graham during the 1928 investigations. The annual toll of seals in the Wash has varied from about 100 to 300, with an average of (say) 200. Havinga (1933) concluded that in Holland an average toll of 1000 per annum was maintained for many years from a computed stock of 4000; but his graph, in fact, shows a slight decline, and a later rise after 3 years of diminished killing during the First World War.

On this basis the Wash population (excluding the Norfolk coast herds), averaging between 800 and 1000, would remain more or less constant with an average kill of about 200. The number killed in 1947 was well over 300. In 1948 about 100 seals from the Yarmouth, Boston and Stiffkey (Blakeney) districts were received by a Norfolk firm, and doubtless the total number killed was considerably greater.

We may therefore give the total normal population in the whole area of the census as between 1000 and 1500 animals. Clearly the census method used is by no means an ideal one for this species. Counting from slow-flying planes should be a method eminently suitable for herds spread out on these flat sand-banks; not only would there be less disturbance, but the whole area could be surveyed over a short period during one low tide, thus eliminating the risk of duplicating counts in individual herds.

Biological Notes

Havinga, with Scheffer & Slipp, have summarized most of what is known of the life history and ecology of *Phoca vitulina* in two widely separated sections of its range; but a few points of interest may be noted from the present inquiry.

There are said to be fewer seals in the Wash during the winter. This may represent merely a splitting up of the herds into smaller groups—a decreased gregariousness—or it may represent a partial migration to the outer coast, occasioned by the migration to deeper water of the bottom fish and invertebrates (e.g. the decapod Crustacea) which is known to occur in winter. The former seems the more likely explanation, since should the latter be true the herds along the coast might be expected to increase in size, or at least to be unaffected, by contrast, which is not so. The herds increase in numbers in the spring, and reach a maximum in June, when the young are born. Scheffer & Slipp mention similar fluctuations on the coast of Washington.

In 1948 the first young were seen, at different sands, on 17 and 18 June; in 1947 young seals were killed in numbers from 23 June. To the writer's knowledge, no one has observed the actual process of birth in this species; should it occur on the tidal sandbanks it must presumably occur at low water, although the pups can swim immediately after birth.

It will be noted from the map that the Norfolk coast herds are larger, while

0°
1°
2°
53°
Scale in miles
10 5 0 10 20
Skegness
The Wash
Burnham Flats
Scolthead
Boston
Hunstanton
Wells
Blakeney
Sheringham
King's Lynn
Gt Yarmouth
Scroby
Seal colonies on the East Anglian coast 1948
The size of each circle indicates the order of size of the colony represented

Fig. 1.

farther apart from each other, than those in the Wash. This is no doubt due to the scarcity of suitable sands along the outer coast, which leads to local concentration. These herds probably disperse farther to feed; seals are reported frequently all along the coast, as at Brancaster harbour and the west end of Scolt Head Island, in and outside the harbour at Wells, off Sheringham, and off Winterton and Palling 'especially when the herring drifters are about'. Reports of seals, including single females with pups, off Orfordness and in the Suffolk estuaries may represent incipient colonization in this region or merely an occasional drift down the coast from the Scroby herd off Yarmouth.

These coast herds seem to have increased considerably of recent years; thus according to one observer the colony on the Woolpack Sand numbered some 50 in 1925, while it is now given as 150, and in spite of persecution the Blakeney herd has steadily increased in numbers. It seems likely that these increases have been due in part to recruitment from elsewhere, but it is impossible to say how static and isolated the separate colonies really are until marking experiments have been carried out on these seals. It should be possible to mark the pups successfully. In the White Sea, pups of *Phoca groenlandica* were marked with aluminium disks pierced through the web of the tail in a similar manner to plaice-marking, and their movements traced from subsequent recoveries (Sivertsen, 1941).

In many parts of its range the common seal is known to ascend rivers to a considerable distance from the sea. Records of seals in the fenland rivers are not uncommon; one was shot in the Great Ouse at Hemingford Abbots (45 miles up the river and just below the first lock) on 16 January 1947, and one frequented the Yare between Reedham and Surlingham from late September to early November, 1947 before it was killed. These and other similar records have all been of immature seals in autumn and winter (August to January), which may indicate that seals of this age wander more than the adults. They cause considerable damage to the stocks of fresh-water fish in such small rivers, and rarely survive for long.

Dr Fraser Darling informs me that the young of grey seals are likewise more prone to wander than the adults.

Summary

A study has been made of the food, population, and some aspects of the ecology of the common seal (*Phoca vitulina* L.) along the East Anglian coast.

Examination of stomach contents of 194 seals killed in the Wash in 1947 confirms earlier evidence that the species here feeds largely on whelks (*Buccinum undatum*). The food is estimated by weight as 92 % molluscs, 4 % fish and 4 % Crustacea. Young seals for 2–3 months after weaning feed almost exclusively on shrimps (*Crangon vulgaris*).

Data derived from six stomachs, together with verbal reports, suggest that

seals on the open coast feed more exclusively on fish, chiefly pleuronectids. This agrees with the findings of other workers in Holland and Washington State, U.S.A., that fish are the primary food animals. It is therefore suggested that in the Wash, where suitable breeding sands are common, the seals have become adapted to feeding on a 'second-class' food in the absence of dense stocks of fish.

Counts of all the seal herds located between Skegness in Lincolnshire and Yarmouth in Norfolk in the summer of 1948 gave as an estimate of the total population 1000–1500 individuals. This agrees broadly with the figure deduced from the number of seals killed annually. Comparison with estimates over the last 25 years shows that the species maintains its numbers in spite of intense persecution, several large herds on the Norfolk coast having in fact noticeably increased.

The herds appear to be sedentary, though a slight spring increase in size, probably due to a more marked gregariousness, has been noted. Immature seals frequently ascend rivers and may therefore be more prone to wander than adults.

The young are born from mid-June in this region.

It is concluded from the results of the food investigations that there is local damage to inshore fisheries, though the main part of the stock probably does not have any serious effect on fisheries for shrimps and shellfish.

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THE SCOTTISH SEAWEED RESEARCH ASSOCIATION

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The production of chemicals from the brown seaweeds is one of the oldest branches of the chemical industry, having its origin as far back as 1720 when soda was first produced from kelp in France, and soon after taken up in Ireland, Scotland and Norway. Until the early nineteenth century this was the only source of this chemical on which the glass and soap industries were built up. When the cheap Leblanc soda later became competitive the industry was able to switch to potash and iodine production, a demand for which had arisen about the same time. This industry reached sizeable proportion, as is evidenced by the fact that in 1820 more than 20,000 tons of kelp were produced in the Outer Hebrides, involving the collecting and burning of about a million tons of cast weed.

History repeated itself again, however, as in the middle of the century cheaper sources of potash and iodine were found, and by about 1870 the industry was struggling for survival. Foreseeing the end, E. C. C. Stanford, the chief chemist of the principal company operating in this field, investigated that part of the seaweed which had been burnt during the previous 150 years in the hope that it might contain further chemicals of potential value to industry. As a result, he discovered alginic acid in 1883, suggested a constitution, and found it to be a colloid not unlike cellulose in composition and properties. Stanford was, however, fifty years in advance of the times and the industry virtually came to an end before the close of the century without any use having been made of his discovery.

As kelp production in the Outer Hebrides and Orkney had been the principal means of livelihood of the inhabitants of these islands, the loss of markets resulted in considerable depopulation, a trend which has continued until recent times.

Many efforts have been made during recent years, however, to prevent this decline and various projects have been suggested to afford the crofters a means of obtaining a livelihood sufficiently attractive not only to stop depopulation but, if possible, to reverse the trend. One obvious possibility was to attempt the establishment of a new industry based on the Islands' seaweed resources, although it was quite obvious that any attempted revival of the old industry to produce the inorganic chemicals soda, potash and iodine would not meet the case. Several things had happened, however, since the demise of the old

industry which suggested that a new one could be built up on modern lines, provided fundamental data were obtained and new techniques developed.

In 1929, C. W. Bonniksen, who was then working in the Chemistry Department of University College, London, reinvestigated the alginic acid discovered by Stanford fifty years earlier, and he conceived the idea that it might be possible to produce cellophane-like material from this algal chemical. In pursuance of this idea, he and a number of his university colleagues formed a company for the purpose of collecting brown seaweed, extracting alginic acid therefrom and converting it into cellophane, Despite almost insuperable difficulties some measure of success had been achieved by 1939, when a small factory was in operation at Bellochantuy on the Mull of Kintyre, although the outbreak of the war put a stop to the commercial fruition of this project. However, the earlier work was not wasted, as after two or three years of war it became obvious to the Government that a substitute for jute hessian required for camouflage purposes was urgently needed; furthermore, it was abundantly clear that the basic starting material would have to be found in Britain.

The Ministries of Supply and Home Security therefore set in train a number of projects and collaborative investigations aimed at developing a camouflage textile from alginic acid which it was hoped could be obtained in adequate quantities from indigenous seaweed. This development involved the design and construction of three factories for the production of alginic acid; the responsibility of establishing these and operating them on behalf of the Government was given to Bonniksen and his colleagues. At the same time, fundamental and technical investigations were carried out in several University and Government laboratories and in the laboratories and workshops of a number of textile firms, aimed at the production first of a yarn from alginic acid and subsequently the fabrication of a textile suitable for camouflage purposes.

Success followed their combined efforts, although by the time that the work was complete the need for this material had decreased, as the Japanese were then being pushed back and their threat to the Indian jute supplies minimized.

As a direct outcome of this wartime work there were three large and well-equipped factories established on the west coast of Scotland, but once the wartime need for alginate fabrics lapsed there was a very grave risk that the new seaweed chemical industry would, after all, fail to become established on a permanent basis. The wartime investigations had revealed many gaps in our knowledge. For instance, little was known about the type, location and availability of the brown seaweeds growing in Scottish inshore waters. Next to nothing was known about the chemical composition of even the common species, and no methods for harvesting the sublittoral brown algae had been developed.

The Scottish Seaweed Research Association was therefore formed towards the end of 1944 at the instigation of the Scottish Council on Industry, the Ministry of Supply, the Scottish Office, the Department of Scientific and Industrial

Research, the Marine Stations, and semi-official and independent organizations interested in seaweed utilization, to provide the basic information on which it was hoped that non-governmental interests could build up an industry based on Scottish seaweed, primarily with a view to bringing useful employment to the crofter population of the Scottish Highlands and Islands.

From the outset it was realized that a combined sociological and applied marine biological experiment of this magnitude required an unconventional approach on the widest possible basis, and the pattern which has been followed is probably unique in the annals of marine science or industrial development.

A programme of research and development was outlined and the problems there defined have subsequently been investigated by the Association's own staff of botanists, chemists, chemical engineers and engineers, and by fifteen University and Government or state-aided laboratories, in close collaboration with the interested industry and the appropriate Government departments and Ministries.

The Seaweed Research Association's early operations were based on accommodation made available by the Chemistry Department of the University of Edinburgh, but the growth of the Association's activities and the University's need for all its laboratory facilities at the termination of hostilities resulted in accommodation having to be found elsewhere. Since 1947 the Association's headquarters have been the Institute of Seaweed Research at Inveresk Gate, an old mansionhouse standing in 11 acres of land which has been converted to house chemical, botanical and engineering laboratories and workshops and the necessary library and office facilities. In addition, four outstations at Oban and Dunbar on the mainland, Kirkwall in Orkney, and Lochmaddy in North Uist, have been set up from which the survey and experimental vessels have operated.

Although the original research and development programme has not yet been completed, considerable progress has been made both by the Association's staff and by its extra-mural collaborators.

Investigations so far completed have covered the development of methods for the quantitative survey of brown seaweed beds (Walker, 1947*a*), and their application to the Scottish littoral (Walker, 1947*b*; Gibb, 1950) and sublittoral zones (Walker, 1947*a*, 1950); the study of ecological factors (Walker, 1948; Moss, 1948, 1950*a*, *b*; Black, 1950*b*; Black & Dewar, 1949), and the determination of optimum conditions of weed growth by controlled culture (Smith & Walker, 1948).

With a view to developing new and extended uses of seaweed and seaweed products, studies of the chemistry of algal chemicals have been made (Percival & Ross, 1948*b*, 1949, 1950*a*, *b* 1951; Chanda & Percival, 1950; Connell, Hirst & Percival, 1950), methods of analysis developed (Cameron, Ross & Percival, 1948; Percival & Ross 1948*a*; Black, Cornhill, Dewar, Percival & Ross, 1950), and determinations of the chemical composition of the

principal indigenous brown algae and its variation with species, season, age, environment, etc., carried out (Black, 1948*a*, *b*, *c*; 1949; 1950*a*, *c*).

Methods have also been developed for the production of such constituents and their derivatives as are found to be of potential technical value (Bashford, Thomas & Woodward, 1950; Black, Dewar & Woodward, 1951), and the value of seaweed as a component of animal feed and as a fertilizer assessed.

As the ultimate success of an industry based on seaweed must depend upon adequate supplies at a reasonable cost, the efforts of the engineering staff have been largely directed to the development of economic harvesting techniques (Mackenzie, 1947; Jackson, 1951) and the determination of optimum conditions of drying, grinding and handling.

The Association is not a commercial organization, but is so constituted that any individual or organization in Britain in any way interested in the utilization of seaweed can become a member by payment of a nominal fee. By this means scientific and technical data as it becomes available can be and is made use of with the minimum of delay by the universities, research organizations and by industry.

The Board of Management of the Scottish Seaweed Research Association has always realized however, that, in addition to being responsible for providing the basic information on which a rural industry can be established, it has the far more important and exacting task of ensuring that this is understood and applied in such a manner as will benefit the rural community without spoliation of any of the nation's natural marine resources.

This has involved the putting into effect of a sizeable public relations and educational programme by means of wide circulation of technical and progress reports, press releases, and semi-popular articles (cf. Jackson 1948), the production and display of informative films and the giving of lectures, radio talks, demonstrations, exhibitions and discussions, and the holding of informal meetings at which the need for balanced conservation techniques has been stressed.

This programme, amongst other things, has been aimed at showing both the crofter and lay public and the interested industry that, largely because of increasing population pressure and consequent depletion of the country's non-renewable mineral reserves, increasing use will inevitably have to be made of our renewable resources (Woodward, 1950*a*, *b*). As Britain's agricultural and forestry techniques are as advanced as any in the world, and as a very high proportion of the land area is already under extensive cultivation, the sea is virtually the only untapped indigenous source of new organic material.

That the operations of the Association and those associated with it have not been without success is indicated by the fact that its original membership has doubled since its formation in 1944; whereas in 1944 there were no companies specifically harvesting seaweed, now there are two about to commence operations. In 1944 there were five companies in Britain using seaweed for

chemical production or agricultural use, now there are eight. There has, in addition, been a significant expansion within the industry during this time, and as a result cast weed is now collected in S. Uist, N. Uist, Benbecula, Barra, Lewis, Tiree, the Orkneys and in the Fraserburgh and Peterhead areas. The total tonnage of seaweed collected in Scotland has increased sevenfold in the last five years, and the total number of collectors has increased sixfold during that time. As a direct outcome of this expansion in the industry there is now no male unemployment in S. Uist.

Alginate production is at the time of writing Britain's major seaweed industry, and this chemical now sells in twenty countries abroad as well as in the home market. British agar production has similarly developed since the end of the war. Whilst accurate figures for the output of the five British alginate and agar-producing firms are not available, it is fairly certain that the industry is producing these chemicals to the value of about £700,000 per annum at the present time, a not inconsiderable portion of which represents wages paid to the seaweed collectors and the operatives employed in the four Scottish seaweed processing factories located near Girvan, Oban and Lochboisdale. As this industry, which is still expanding, has virtually been built up since the war, it can reasonably be claimed that the £120,000 so far provided by the Treasury from the Development Fund, together with the additional £11,500 subscribed by industry and private interests to further the work of the Association, has been a sound investment, for only as the result of this research and development work and that of the Association's member firms has this been made possible.

Much, however, still remains to be done, as commercial outlets for algal chemicals other than alginic acid and agar have yet to be established, and the mechanical harvesting of Scotland's 10,000,000 tons of brown seaweed and adequate resources of red weed have yet to be carried out on the commercial scale.

A list of publications so far issued or submitted for publication under the auspices of the S.S.R.A. (up to October 1950) is herewith appended.

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ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

The Equilibrium Function of the Otolith Organs of the Thornback Ray

By Otto Lowenstein and T. D. M. Roberts

Journ. Physiol., Vol. 110, 1949, pp. 392–415.

In the labyrinth of *Raja* the otolith organs in the utriculus, sacculus and lagena contain sense-endings with equilibrium function. The discharge frequencies from these sense-endings undergo changes when the skull is tilted.

In some endings each position of the skull is associated with a characteristic discharge frequency regardless of the direction from which this position is reached (stato-receptors proper).

In other endings the succession of frequencies and the position of maximum activity was found to be dependent on the direction of tilting, but the discharge activity reverted to some constant value when and wherever the skull was brought to rest (out-of-position receptors). Single functional units were generally found to respond to lateral as well as to fore-and-aft tilting.

The ranges of response types for the utriculus and sacculus overlap. Two types may be distinguished: those with their maximum frequency of discharge in the 'side-up' and 'nose-up' positions, and those with maximum frequency in 'side-up and 'nose-down'. The absence of stato-receptor preparations with a maximum frequency of discharge in the 'side-down' position is unexpected.

In the lagena the maximum frequency was always in or near the normal position, the frequency falling off fairly sharply on either side of the maximum (into level receptors). This organ is thus particularly suited for mediating stabilization around the normal position. O.L.

The Control of Retinal Pigment Migration in *Leander serratus*

By Francis G. W. Knowles

Biol. Bull. Woods Hole, Vol. 98, 1950, pp. 66–80.

A study was made of the relative importance of hormonal control and a direct response to illumination in the movements of the distal and proximal retinal pigments in *Leander serratus*. Animals from which the sinus glands had been

removed were studied in darkness and under illumination; in these animals the distal pigment remained in the dark-adapted position both in darkness and under illumination; the proximal pigment of operated animals continued to show normal positional changes in response to illumination.

In one series of animals one eye was covered with modelling clay and the other was exposed to illumination; in another series the animals were maintained in light-proof boxes with one eye only projecting through and exposed to illumination. In these experiments the distal and proximal pigments in the exposed eyes showed a greater light-adaptation than in the covered eyes; the difference was especially noticeable in the case of the proximal pigment. The present work suggests therefore that the proximal retinal pigment in *L. serratus* responds directly to change of illumination and is not controlled by the sinus gland; the distal pigment appears to be under sinus-gland control but the responsiveness of the pigment cells to the sinus-gland hormone seems to be increased by illumination. F.G.W.K.

BOOK REVIEW

Nets. How to Make, Mend and Preserve them

By G. A. Steven

Routledge & Kegan Paul Ltd., 1950. Price 5*s*.

Mr Steven has well earned the thanks of all who work with, or are interested in, nets and netting. His brilliant little manual should be welcomed by Libraries, Technical Institutes, Sea Scouts, and Fishermen, whether amateurs, learners, or professionals. The most experienced trawlerman will find in it much interest, and fresh knowledge. Coming as it does from a practical scientist on the staff of the Laboratory of the Marine Biological Association, with a background of experiments with net preservatives, must stamp the book with the highest of hall-marks. Mr Steven's travels and his work on colonial fisheries' development have enabled him to bring to his book fresh angles and methods. In simple language he takes one through the routine of net-making, mounting, and mending; he has a chapter on knots and hitches, another on preservation and even one on how to make such things as rabbit purse nets, garden hammocks, tennis nets and a lady's shopping bag.

I found the book, once picked up, difficult to put down. I seldom remember having seen so good a 5*s*. worth.

With some 160 simple and clear illustrations this little manual might well be described as the perfect *vade mecum* on nets. M.H.N.

INDEX

A

Abra, 167–75, 280
— *alba*, 167–79
— *nitida*, 170–9
Acanthias vulgaris, numbers in trawl catches, 652–9
Acartia, 196–8
— *clausi*, 195, 239; biology of, 393–438
Acetobacter xylinum, cellulose synthesized by, 381
Acipenser sturio, 264
Acrochaetium endozoicum, 260
Acrocnida brachiata, 167
Aglantha digitalis, 649
Agonus cataphractus, 710; food of common seal, 711
Alcyonidium, 260
— *hirsutum*, 258, 260
Algal records for the Plymouth region, 257–61
Aloidis gibba, 168–78
Ammodytes, food of common seal, 709
— *cicerellus*, 533
— *lanceolatus*, 85
— *marinus*, 86
— *tobianus*, 85
Ammotrypane, 173
Ampelisca, 173–9, 248, 528
— *brevicornis*, 167–71, 238, 248
— *diadema*, 193–8, 238–9, 248
— sp. (allied to *brevicornis*), 248
— *spinipes*, 175, 188–95, 238–9, 248
— *tenuicornis*, 171–4, 238, 248
Amphicteis sp., 178
Amphilochus neapolitanus, 248
Amphioxus, 84
Amphipoda, notes on Plymouth fauna, 247–53
Amphithoë vaillanti, 253
Amphitrite, 178, 193–8, 238
— *edwardsi*, 171
Amphiura filiformis, 168–79
Anchialina, 194
— *agilis*, 238
Anomia ephippium, 301
Aora typica, 252
Apherusa bispinosa, 250
— *cirrus*, 251
— *henneguyi*, 188–93, 238–9, 250, 528
— *ovalipes*, 193, 238–9, 250
Aphrodite, 177, 678
Aplysia punctata, 531
Arenicola assimilis, 2
— *claparedii*, anatomy of body wall and appendages, 1–44
— *cristata*, 9, 41, 42
— *ecaudata*, anatomy of body wall and appendages, 1–44
— *grubii*, 2, 37
— *loveni*, 40
— *marina*, 268, 628, 661–79; anatomy of body wall and appendages, 1–44; spawning period in, 332
Ascocyclus sphaerophorus, 258
Ascophyllum, 441–2, 465, 488, 493–4, 497
— *nodosum*, cellulose content of, 383–6; uptake of tracers by, 531
Asterias, preying on mussels, 127
— *forbesi*, parasitized by *Orchitophrya*, 619, 623
— *rubens*, 655; parasitized by *Orchitophrya*, 528, 619–24
— *vulgaris*, parasitized by *Orchitophrya*, 619
Asterina gibbosa, development of gonads, 263–4
Astropecten, 173
Atractophora hypnoides, 260, 527

B

Bacteria, production of suspended, 124–5; 129–32; production in sea-floor, 128–32
Balanoglossus clavigerus, 625, 635–6
Balanus amphitrite, 283
— *balanoides*, 283; larvae in plankton, 72–80
— *crenatus*, 299–302; larvae in plankton, 72–80
— *improvisus*, 283–94
Balistes capriscus, 254
Barnacle larvae, sampled by Hardy Continuous Plankton Recorder, 73–80
Bathyporeia, 165–78
— *elegans*, 167
— *guilliamsoniana*, 167
Biddulphia sinensis, 671
Bispira volutacornis, response to light, 303–7
Bittium reticulatum, 574, 583
Bolbocoleon piliferum, 257
Bottom fauna, production of, 126–8
Branchiomaldane, 2
Branchiomma vesiculosum, 530; responses to photic stimulation, 303–20
— *vigilans*, response to light, 303
Branchiomonas submarina, 257
Buccinum undatum, 583; food of common seal, 707–12, 716
Bullinella cylindracea, 177

C

Calanus, 117–20, 195–7
— *finmarchicus*, 117–20, 195–8, 238–9, 405, 411, 413, 438; grazing rate of, 695–706; respiration of, 681–93
Callianassa, 711
— *subterranea*, 178–81
Callionymus, 191–8, 238
— *fasciatus*, 533
— *lyra*, 247, 533
— *maculatus*, 533
Calliopius laeviusculus, 251
Candacia, 197
Cantharus lineatus, 254
Carcinus maenas, food of common seal, 709
Cardium, 175
— *aculeatum*, 167–74
— *echinatum*, 173
— *edule*, 268; food of common seal, 709, 711
— *ovale*, 169
— *tuberculatum*, 167
Carpomitra costata, 259
Castagnea zosterae, 258
Cellaria, 167–70
Cellulose content of Laminariaceae and Fucaceae, 379–87
Centropages, 117
— *hamatus*, 395, 408, 438; grazing rate of, 698–706; respiration of, 681–93
— *typicus*, 195, 239; biology of, 393–438; respiration of, 681–93
Cerianthus lloydi, 168–75.
Cerithiopsis barleei, 568
— *tubercularis*, life history and morphology of, 567–86
Cerithium telescopium, 585
— *vulgatum*, 585
Chaetoceros, food of copepods, 704
— *gracilis*, chlorophyll content of, 613
— *vanheurckii*, chlorophyll content of, 613
Chaetopterus variopedatus, irrigation of burrow in, 661–80
Cheirocratus assimilis, 238, 251
Chione fasciata, 169–80
— *striatula*, 167–79
Chlamydomonas, 612, 686; chlorophyll content of, 613, 616–17; food of copepods, 697–705
Chlamys opercularis, 167, 528, 568
Chlorella, chlorophyll content of, 613, 616–17
— *pyrenoidosa*, 103
Chlorophyll estimations of phytoplankton, 609–18
Chondrus, uptake of tracers by, 531
— *crispus*, 258, 260
Ciliata mustela, 264
Cladophora, 299
Clupea harengus, food of common seal, 711
— *pallasii*, 711
— *pilchardus*, spawning in the English Channel, 91–5
— *sprattus*, 710
Coccolithophores, 98
Common seal, status of, 707–17
Conger conger, 517
Conilera cylindracea, 195, 238–9
Copepods, biology of small, 393–438; grazing rate of planktonic, 695–706; respiration of planktonic, 681–93
Coremapus versiculatus, 170
Corycaeus anglicus, biology of, 393–438
Corynophlaea crispa, 258
Corystes cassivelaunus, 167–75, 238
Coscinodiscus centralis, 612, 671; chlorophyll content of, 613, 616, 617
Cottus scorpius, food of common seal, 711
Crago, 711
Crangon, 197
— *vulgaris*, 193–5, 238–9; food of common seal, 707–12, 716
Crepidula fornicata, 180
Cryptocoelis sp., 177
Crystallogobius, 197
— *nillsoni*, 191, 238
Ctenolabrus, 191, 238
Cucumaria, 238
— *elongata*, 169–78
Cultellus pellucidus, 168, 168–79
Current meter, 588
Cypraea arabica, 581
Cystoseira ericoides, 259

D

Dasychone bombyx, 175; response to light, 303
Demersal fish, production of, 125, 129–32
Dentalium sp., 175
Desmarestia dudresnayi, 259
Dexamine thea, 252
Diastylis, 167–74, 238
— *laevis*, 167–71
Diatoms, effect on barnacle development, 79–80; production of, 98 *et seq.*
Dicrateria inornata, 612; chlorophyll content of, 613, 616, 617
Dictyopteris membranacea, 259
Dictyota, dichotomy in, 458
Didemnum maculosum, 389
— *perforatum*, 389
Dinoflagellates, production of, 98 *et seq.*
Dinophysis, 197
Diodora apertura, 573, 580
Diplodonta rotundata, 175
Diplosoma, 391

Ditylum brightwellii, food of copepods, 696–705; size of, 98
Donax vittatus, 165–67
Dosinia exoleta, 174
— *lupinus*, 170–4
Drepanopsetta, 187
— *platessoides*, numbers in trawl catches, 652–9
Dudresnaya verticillata, 260
Dynamena pumila, 258

E

Ebalia, 179
Echinocardium cordatum, 165–79
Echinoclinum, 391
Echinocyamus pusillus, 172–5
Ectocarpus sandrianus, 299
Eledone cirrosa, identity confused with *Octopus*, 364–5; eggs of, 366, 372–3
Elminius modestus, gregariousness during settlement of, 281–97.
Endodictyon infestans, 258
Ensis, 165–78, 529; identification of British species of, 639–47
— *arcuatus*, 639–47, 529
— *ensis*, 639–47, 529
— *siliqua*, 639–47, 529
Enteromorpha, 257, 294; and germination of *Fucus*, 448
Eone, 174
— *nordmanni*, 171
Epicladia flustrae, 258
Erichthonius brasiliensis, 238
Erythropeltis discigera, 260
Eteone sp., 171
Euchaeta norvegica, respiration of, 681–93
Eudistylia polymorpha, response to light, 303
Eudoxids, 92
Eupagurus, 168–77; food of common seal, 709
— *bernhardus*, 168–71, 187–95, 238–9; food of common seal, 710
— *cuanensis*, 169–70
— *prideauxi*, 238
Eurystheus maculatus, 238, 252
Euterpina, 196
— *acutifrons*, 394, 408
Euthemisto compressa, 649
Euthynnus pelamys, 254

F

Fagotia esperi, 585
Fertility of the sea, evidence of changing, 132–5
Fibrous glass surfaces, effect on settlement of organisms, 299–302
Ficulina ficus, 568
Fish, seasonal abundance of young, 133–5
Fishes, internode lengths in nerves of, 517–18
Flagellates, production of, 98 *et seq.*
Flustra, 260
Fucaceae, seasonal variation in cellulose content, 379–87
Fucus serratus, 258; biological study of, 439–514; cellulose content of, 380; defoliation of, 481–4; depopulation of, 484–7; frond development in, 455–65; germination of, 443–9; growth-rate, 449–53; repopulation in, 488–97; reproduction in, 470–6; uptake of tracers by, 488–97
— *spiralis*, cellulose content of, 383–6; growth rate in, 453; occurrence with *F. vesiculosus*, 465; zone of, 441–2
— *vesiculosus*, biological study of, 439–514; cellulose content, 380; defoliation, 481–4; depopulation, 484–7; frond development, 455–65; germination, 443–9; growth-rate, 449–53; repopulation, 488–97; reproduction, 470–81; uptake of tracers by, 531; vesicle formation, 465–70; var. *divaricatus*, 469; var. *evesiculosus*, uptake of tracers by, 531; var. *sphaerococcus*, 469; var. *vadorum*, 466, 469.

G

Gadus callarias, numbers in trawl catches, 652–9
— *merlangus*, food of common seal, 707–12; numbers in trawl catches, 652–9
— *minutus*, 247–8, 528, 533; age and growth of, 198–235; bionomics of, 185–239; food of, 186–98; numbers in trawl catches, 652–9
Gaidropsarus tricirratus, 264
Galathea, 187–97, 533
— *dispersa*, 193, 238
— *intermedia*, 193–8, 238–9
— *strigosa*, 238
Gammarus locusta, 167
— *zaddachi oceanicus*, 528
Gari ferroensis, 175
Garstang, Walter, obituary, 561–6
Gibbula magus, 168–71
Giffordia sandriana, 258
Gigartina, uptake of tracers by, 531
— *teedii*, 260, 527
Glossobalanus marginatus, 625
— *minutus*, 625, 636
— *ruficollis*, 635
Glycera, 169–78
— *convoluta*, 169–75
Glycimeris glycimeris, 180
Gobius minutus, food of common seal, 709–10

Goniada, 193–8, 238–9
— *maculata*, 177
Gonoplax rhomboides, 169
Grateloupia filicina, 260
— *minima*, 260
Great West Bay, bottom fauna of, 163–83
Gryphaea virginica, spawning stimulus in, 332
Gymnammodytes capensis, 83–89, 533
— *cicerelus*, 83–89
— *semisquamatus*, 533; in the Plymouth area, 83–89
Gymnodinium, chlorophyll content of, 612–13, 616–7

H

Haematopus fuliginosus, 40
Halichoerus grypus, 712
Halichondria panicea, 577
Haplospora globosa, 258
Hardy plankton recorder, barnacle larvae sampled by, 73–80
Harmothoë lunulata,174
Harpinia antennaria, 174, 248
Haustorius arenarius, 248
Hemimysis, 120
Hemiselmis rufescens, chlorophyll content of, 613, 616–17
Hermella ascolata, response to light, 310, 317
Heterosepiola atlantica, 238
Hippolyte varians, 238–9
Hippomedon sp., 178
Homarus vulgaris, 530
Hyalinoecia bilineata, 170
Hydroides dianthus, 630; response to light, 303–11
— *uncinata*, response to light, 303
Hymeniacidon sanguinea, 568, 573, 577

I

Inachus dorsettensis, 238
Iphimedia obesa, 238
Iphinoë trispinosa, 165–71
Isochrysis galbana, chlorophyll content of, 616–17

L

Labidocera wollastoni, 197, 238
Labidoplax digitata, 167–71
Laevicardium crassum, 180
Lagis, 710
Lamellaria, 584
— *perspicua*, 572, 581, 583
Laminariaceae, seasonal variation in cellulose content, 379–87; seasonal variation in weight and chemical composition, 45–72
Laminaria zone, 441–2
— *cloustoni*, 262; cellulose content of, 380–6; seasonal variation in weight and chemical composition, 45–72
— *digitata*, 257, 261–2, 527; cellulose content, 383–6; uptake of tracers by, 531; weight and chemical composition, 45–72; zone of, 442, 493
— *flexicaulis*, 46; cellulose content of, 379
— *ochroleuca*, 259; additional records in Plymouth area, 261–2
— *saccharina*, 258, 261; cellulose content of, 379–86; seasonal variation in weight and chemical composition, 45–72
Lanice, 167–77
— *conchilega*, 173–8
Laomedea flexuosa, 301
Lauderia borealis, food of copepods, 696, 703, 704, 705
— *glacialis*, growth of, 99
Leander serratus, 197; control of retinal pigment migration in, 727–8
Lepidasthenia argus, 168–9
Leptocheirus pilosus, 253
Leptomysis gracilis, 194 *et seq.*, 238–9
Leptosynapta inhaerens, 171 *et seq.*
Leptotheca, emended definition of genus, 264
— *vikrami*, new species, 264
Lessonia flavicans, laminarin absent in, 51
Leucothoë, 238, 249, 528
— *lilljeborgi*, 167, 249
— sp. (allied to *richiardi*), 249
— *spinicarpa*, 249
Liparis montagui, 710
Lissoclinum, 391
— *argyllense*, new ascidian from Scotland, 389–92
— *aureum*, 391
Lithophyllum hapalidioides var. *confinis*, 260
Littorina, feeding on *Fucus* eggs, 446
— *saxatilis*, 583
Loligo, 516; food of common seal, 709; giant fibres of, 529; phototropism of larva, 365
Lumbriconereis sp., 169–75
Lutraria sp., 167–81
— *lutraria*, 169–80
Lycastis quadraticeps, hermaphrodite nereid, 354
Lysianassa ceratina, 247

M

Mackerel eggs, 92, 94; fishery, 531–3
Macoma, 280
— *balthica*, 268
Macrocystis pyrifera, laminarin absent in, 51
Macropodia, 173
— *longirostris*, 238
Mactra corallina, 173–7
Maera, 173
— *othonis*, 238
Magelona papillicornis, 165–76

Marthasterias glacialis, 261
Melanopsis dufourei, 585
Melinna, 172–7
— *palmata*, 168–78
Melita gladiosa, 232
— *hergensis*, 251
— *pellucida*, 252
Melphidippella macra, 251
Merluccius hubbsi, 224, 232
— *merluccius*, 224, 232; numbers in trawl catches, 652–9
Mesogloia lanosa, 258, 527
Metridia, 196
— *lucens*, 395, 411, 438
Metridium, 655
Microcalanus, 395
Microdeutopus chelifer, 252
— *damnoniensis*, 252
Microprotopus maculatus, 252
Monoculodes, 238, 250, 528
— *carinata*, 238
— sp. (? *tessalatus*), 250
Montacuta ferruginosa, 167–76
Muggiaea atlantica, 92, 94
— *kochi*, 92, 94
Munida bamffica, 193, 238
Mya arenaria, response to light, 308–9
— *truncata*, 171
Myliobatis aquila, 254
Myriocladia lovenii, 258
Myriotrichia densa, 259
— *repens*, 259
Mysella bidentata, 173–8
Mysia undata, 167–71
Mytilus, 673
— *edulis*, food of common seal, 709–10
Myxicola infundibulum, conduction velocity in relation to axon diameter, 265; function of giant axon of, 265; response to light, 303
Myxosporidia, new species from Plymouth, 264

N

Nassa reticulata, 177
Natica, 195, 584
— *catena*, 176, 238–9
Naucrates ductor, 254
Neanthes succinea, epitoquous form of, 353–4
— *virens*, response to light, 310
Nebalia bipes, 238
Nematonereis unicornis, 169–71
Nephrops norvegicus, numbers in trawl catches, 652–9
Nephthys, 165–79
Nereis, 167–78
— *diversicolor*, irrigation of burrow in, 661–79; reproduction and development, 321–60
— *japonica*, green colour at maturity, 328
— *limbata*, reproduction and development contrasted with *N. diversicolor*, 332, 335, 355
— *longissima*, 170 *et seq.*
— *massiliensis*, hermaphrodite nereid, 354
— *megalops*, 335
— *pelagica*, development contrasted with *N. diversicolor*, 339 *et seq.*
— *virens*, 675
Nereocystis luetkeana, laminarin absent in, 51; composition of haptera, 64, 65
Nerine, 167
Nerve, advances in physiology of peripheral, 241–6; effect of calcium on giant fibres, 516
Nets. How to make, mend and preserve them, 729
Nika edulis, 177–8
Nitzschia, uptake of tracers by, 531
— *closterium*, 610, 671, 103; food of copepods, 703–5; pigments of, 101
— *closterium* forma *minutissima*, chlorophyll content of, 613–7; food of copepods, 704
— *seriata*, chlorophyll content of, 613, 615
Notomastus latericeus, 171–4
Nototropis falcatus, 238
— *swammerdami*, 167
Nucula, 195
— *nitida*, 167–79, 238–9
— *radiata*, 170
Nyctiphanes couchi, 195, 238–9

O

Octopus vulgaris, distribution in British waters, 361–78; development and larvae, 366–72; source of population in British waters, 372–6
Oithona nana, biology of, 393–438
— *similis*, biology of, 393–438
Oncaea venusta, biology of, 393–438
Ophelia bicornis, settlement of larvae, 128, 301–2, 526–7
Ophiodromus flexuosus, 179
Ophiopsila annulosa in the Plymouth area, 81
— *aranea*, 81
Ophiothrix fragilis, 170, 528
Ophiura, 655
— *texturata*, 175, 238
Orchitophrya stellarum, 528; parasite of *Asterias*, 619–24
Orchomene humilis, 248
Orchomonella nana, 238, 248
Ostrea edulis, 168, 281–2
— *virginea*, 630
Owenia, larvae affected by air bubbles, 149
— *fusiformis*, 167–79

P

Palinurus vulgaris, 530
Pallasia murata, 170–5, 193, 238
Pandalina brevirostris, 195, 238–9
Pandalus, 187
— *montagui*, 197; food of common seal, 709
Panoploea eblanae, 250
— *minuta*, 238, 250
— *obesa*, 250
Paphia rhomboides, food of *Octopus*, 363
Paracalanus parvus, biology of, 393–438
Peachia hastata, 167–71
Pecten maximus, 167
Pectinaria, 171–80
— *auricoma*, 169–75
— *koreni*, 164–75
Pelagic fish, production of 122–4, 129–32
Pelvetia zone, 441–2
— *canaliculata*, cellulose content of, 383–6
Pereionotus testudo, 250
Perinereis cultrifera, 252, 352
— *marionii*, 331, 630
Perrierella audouiniana, 247
Peyssonnelia atropurpurea, 260
Phaeosphaera perforata, 610
Phascolion strombi, 168–78
Phascolosoma, 178
— *elongatum*, 169
— *vulgare*, 169–70
Pherusa fucicola, 251
Philine, 173
— *aperta*, 169–71, 238
Philocheras bispinosus, 193–5, 238–9
Phoca foetida, 712
— *groenlandica*, 712, 716
— *vitulina*, food of, 707–12; population, 712–4; status of, 707–17
— *vitulina richardii* food of, 711
Pholadidea, 81
Phosphagen, annelid, 515
Phosphorus cycle in the English Channel, 145–62
Phtisica marina, 193–8, 238–9, 253
Phyllochaetopterus, 179
Phyllodoce, 167–74
— *maculata*, 173–8
Phytoplankton, production of, 98–112, 129–32; seasonal changes in, 609–18
Pilchard, 91–5
Pisces, notes on Plymouth fauna, 254–5
Planorbis, 584
Platynereis dumerilii, development compared with *Nereis diversicolor*, 347–54
Plectonema battersii, 257
Pleurobrachia, 117
Pleuronectes, food of common seal, 707–12
— *cynoglossus*, numbers in trawl catches, 652–9
— *flesus*, food of common seal, 710–11
— *platessa*, numbers in trawl catches, 652–9; preying on polychaetes, 317
Plumularia, 260
Plymouth marine fauna, notes on, 247–55
Plymouth marine flora, notes on, 257–62
Podoceropsis sophiae, 252
Podocerus variegatus, 253
Podon, 195–7
Polygordius, larvae affected by air bubbles, 149
Pomatoceros triqueter, 301; response to light, 303
Poor-Cod, see *Gadus minutus*, 185–239
Porcellana, 187–98
— *longicornis*, 173, 193–7, 238–9
— *platycheles*, 193, 238
Portunus, 178, 187–98, 239, 533, food of common seal, 709–10
— *depurator*, 193, 238
— *holsatus*, 238
— *pusillus*, 193, 238
Potamilla reniformis, response to light, 303–11
Prasinocladus lubricus, 257
Processa canaliculata, 187–98, 238–9, 533
Production of living matter in the sea off Plymouth, 97–137
Protodrilus, settlement of larva, 128
Protoglossus, 634
Protula intestinum, response to light, 303
Psammechinus miliaris, 168–78
Psammosolen chamasolen, 174
Pseudocalanus, 196–7
— *elongatus*, 195–6, 239, 533; biology of, 393–438
— *minutus*, grazing rate of, 698–706
Pseudocuma cercaria, 167
Pseudoprotella phasma, 238, 253
Ptychodera bahamensis, 625
Pyramimonas grossii, 257

R

Raia clavata, 517
Raniceps raninus, 254
Retusa sp., 171–4
Rhodochorton rothii, 610
Rhodymenia, uptake of tracers by, 531
Rocinela danmoniensis, 238

S

Sabella micropthalma, response to light, 303
— *spallanzanii*, response to light, 303–4
Saccoglossus, 634
— *cambrensis*, breeding of, 626, 632–4,
— *horsti*, spawning behaviour of, 625–38
— *kowalevskyi*, 625, 635–6
— *otagoensis*, 625, 635
— *pusillus*, 625, 635
— *pygmaeus*, 626

Sacchoriza bulbosa, 261; laminarin in, 51
Sagartia sp., 167–74
Sagitta elegans, 92, 94, 135
— *setosa*, 92, 94, 135, 413
Salmonid, food of common seal, 709
Sarda pelamys, 254
Scala communis, 574, 583
Scalibregma, 173–8
— *inflatum*, 169–75
Scoloplos armiger, 167–74
Scombrops chilodipteroides, 214
Scottish Seaweed Research Association, 719–23
Scrobicularia, 280
Scyliorhinus canicula, 517
Scytosiphon lomentaria, 259
Sepia, nerve fibre of, 529
— *officinalis*, food of common seal, 711
Serpula vermicularis, response to light, 303–8
Serranus cabrilla, 254
Seven Stones Lightvessel, water movements and winds at, 587–608
Sigalion, 173–8
— *mathildae*, 165–75
Sinuolinea rebae, new species, 264
Skeletonema costatum, 73, 80, 697
Socarnopsis crenulata, 247
Solea solea, 264
— *vulgaris*, preying on polychaetes, 317
Solen ensis var. *magna*, 639
Spartina townsendii, 626
Sphacelaria furcigera, 259
Spiophanes bombyx, 171–4
Spirontocaris cranchi, 238
Spisula, mortality of dense population, 127
— *elliptica*, 173
— *solida*, 176
— *subtruncata*, 165–71
Spondylothamnion multifidum, 260
Squid, effect of sodium ions on activity of giant axon, 516; effect of temperature on activity of giant axon, 516
Staurocephalus, 169
Stenogramma interruptum, 260
Stenothoë, 249
— *monoculoides*, 249
— sp. (allied to *spinimana*), 249
— *spinimana*, 249
— *valida*, 249, 528
Sthenelais, 179
— *boa*, 167–78
— *limicola*, 173–9
Stictyosiphon soriferus, 259
Stilophora rhizodes, 259
Stylaroides flabellata, 174
Suspended matter of sea water, 139–43
Synapta, 178
Syngnathus, food of common seal, 709

T

Tellina donacina, 175–9
— *fabula*, 165–78
— *tenuis*, population-dispersion in, 267–80
Temora, 117, 195–8
— *longicornis*, 239; biology of, 393–438; grazing rate of, 698–706
Tenebra triseriata, 584
Tetrodon lagocephalus, 254
Thalassiosira gravida, 671; chlorophyll content of, 613–17; growth of, 99
— *Nordenskioldii*, growth of, 99
Themisto libellula, 712
Theragra chalcogramma, 194
Thornback ray, equilibrium function of otolith organs of, 727
Thyasira flexuosa, 171–9
Thyone roscovita, 170
Tivela stultorum, 630
Tomopteris, 112, 117
Torpedo ocellata, 517
Trawl catches, statistical study of variability in, 649–60
Triforis (= *Triphora*) *montrouzieri*, 567
Trigla, 191, 238
Triphora perversa, life history and morphology of, 567–86.
Trivia arctica, 572
— *monacha*, 572
Trygon pastinaca, 254
Tryphosa sarsi, 247
Tubularia, 287
— *larynx*, 301–2
Turritella communis, 166–81, 238–9, 574, 583, 584

U

Ulothrix flacca, 299
Ulva, 295; and germination of *Fucus*, 448; uptake of tracers by, 531
Upogebia, 194, 238, 711
— *stellata*, 175
Urothoë elegans, 238, 248
— *grimaldii*, 167–71

V

Velutina, 584

X

Xenococcus schousboei, 257

Y

Yoldia myalis, 711

Z

Zeus faber, 264
Zooplankton production, 112–22, 129–32
Zostera, 258, 259; decline of, 527; occurrence of *Octopus* in beds of, 363
Zschokkella russelli, new species, 264
— *sturionis*, 264

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